Morphometric Analysis of the Broad-snouted Caiman (*Caiman latirostris*) an Assessment of Individuals Clutch Body Size, Sex Age and Area of Origin

By

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To Denise, Bob, and Cadu,

with whom it has been wonderful to share this and other journeys

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MORPHOMETRIC ANALYSIS OF THE BROAD-SNOUTED CAIMAN (*CAIMAN LATIROSTRIS*) AN ASSESSMENT OF INDIVIDUALS CLUTCH BODY SIZE, SEX AGE AND AREA OF ORIGIN

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Three consecutive questions are tested in the current morphometric study of the broad-snouted caiman (*Caiman latirostris*) Is there a significant morphometric variation related to *clutch effect body size sex age, area of origin* and *environment*? Can the group to which a specific individual belongs be predicted? And last, if it is possible to efficiently predict an individual s group using *all* morphometric variables recorded, is it possible to reduce the number of variables without significantly losing efficiency? Cranial and body morphometric variables were recorded from captive and wild animals. MANOVA linear discriminant analysis with cross-validation PCA and best subset regressions are used in order to answer the questions above. Exploratory studies of relative growth and allometry of reproduction were used to develop models of age estimation, sexual dimorphism and clutch discrimination.

Log-transformation of data significantly improved sexual dimorphism perception through the reduction of the scaling effect among variables. Except for body mass log transformation did not significantly improve data analysis in relative growth studies Ratios between variables were consistently less efficient at detecting differences between groups than direct measurements Multivariate morphometric models are consistently more efficient than univariate growth curves for determining age of animals Sexual dimorphism in cranial morphometry of broad snouted caiman can be detected even in young individuals However it is frequently impossible to isolate gender from other sources of variation, such as clutch, age body

size, area of origin, and environment. There is a positive correlation between female body size and egg size, hatchlings' body size and clutch mass. There is a significant negative correlation between female body size and the relative clutch mass (clutch mass / female body mass). Clutch discrimination based on clutch affect and female family effect (matrilineal lineage) can be used to establish parentage among individuals in small wild populations and captive breeding programs. There is a significant cranial morphometric variation among animals from different study sites. This may be related to some level of reproductive isolation, which may be related to habitat fragmentation. Captive animals present relatively broader snout, cranium, mandible, and external nares, and relatively longer mandibular symphysis than wild individuals.

CHAPTER 1
INTRODUCTION

The broad-snouted caiman (BSC) is a small endemic South American crocodilian. The species inhabits wetlands associated with the Paraná and São Francisco River systems in Brazil, Paraguay, Bolivia, Uruguay, and Argentina, and also the small coastal river drainages from the northeastern Brazil to northern Uruguay (Groombridge 1982, 1987). Its most widespread common names are *jacaré-de papo-amarelo* ("yellow throated caiman") in Brazilian Portuguese and *yacare-de-hocico-ancho* ("broad-snouted caiman") in the Spanish language countries where it lives. As its English and Spanish common names indicate, its most conspicuous characteristic is the broad snout, relatively the broadest among all crocodilians (King and Burke 1989).

The State of São Paulo, Brazil, comprises the central region of the BSC geographic distribution. However, it has lost approximately 95% of its original ecosystems (Victor 1975). The Tietê River – the main river system of São Paulo – has been virtually completely dammed for the construction of hydroelectric stations, and so have its most important tributaries (Diegues 1994). The original net of small wetlands of São Paulo – now severely reduced – has possibly served as the linkage between northern and southern populations of the species. The local extinction of BSC in São Paulo could have a deleterious effect for the species as a whole. On the other hand, caimans' apparent capacity to colonize man-made habitats may be significantly important for their conservation (Verdade and Lavorenti 1990, de la Ossa Velasquez 1994). Long-term studies of this process might help us to understand how caimans respond to environmental changes and how can we deal with similar situations in the future.

As Caughley (1994) elegantly stated, conservation biology has two main subjects: the declining-population paradigm which deals with the cause of smallness and its cure, and the small-population paradigm which deals with the effect of smallness on the persistence of a population. The later seems to be the best approach to the study of the colonization process of BSC on new available habitats. The causes of smallness are irrelevant in this case, but its effects on the persistence of the populations are of major concern. How does the colonization process affect the behavioral-ecology of the species like its dispersion and mating system? How is the population

structure and dynamics affected during the colonization process in terms of sex ratio, age structure and sexual maturity? All these variables would affect the persistence of the population and all these questions would be relevant.

Traditionally, long term field studies are required to understand the basics of a population structure and dynamics (Likens 1989). Time and budget constraints are therefore their main limiting factor. Molecular techniques have been recently developed that yield surprising and relatively fast results not only on genetics but also on behavioral-ecological studies of wild species (Avise 1994). However, although their costs are decreasing, they can still be prohibitive when large sample sizes are used. In addition, expensive equipment and specialized personnel are needed.

Establishing the sex and age of an individual is the first step in the definition of the sex ratio and the age structure of a population (Dunmick and Pelton 1996). The recent development of user-friendly statistical softwares has permitted a considerable advance in the use of multivariate statistical analysis on morphometric studies (Reyment *et al.* 1984). Intra specific analyses of sexual dimorphism and ontogenetic variation using such techniques can be extremely useful to field studies of small populations. When secondary sexual characteristics are not evident, the use of morphometric analysis of sexual dimorphism can be essential to the determination of the population sex ratio (Giles and Elliot 1963). Similarly, morphometric and allometric analysis of growth can be used for the development of age estimation models for individual animals.

Living crocodilians can be sexed by direct observation of the sex organs in the cloaca (Chabreck 1963, Brazaitis 1968, Allistead and Lang 1995). Cranial morphometry can also be used in the sex discrimination of preserved materials (Hall and Portier 1994). Sex in crocodilians is determined by the temperature of incubation (Ferguson and Joanen 1982, and Lang and Andrews 1994) with no sex chromosomes found in cytological studies (Cohen and Gans 1970). Temperature of incubation may also affect embryonic development (Deeming and Ferguson 1989), incubation period (Webb *et al.* 1987), post-hatching growth pattern (Joanen *et al.* 1987, Webb and Cooper-Preston 1989), pigmentation, and thermoregulatory behavior of hatchlings and young (Deeming and Ferguson 1989).

However, there seems to be a pronounced variation caused by the clutch of origin on the pattern of the temperature-sex determination (called "clutch effect" by Lang and Andrews 1994) and possibly on the growth pattern of hatchlings and young. If true, then animals from different clutches could exhibit a significant variation not only in body size but also in body shape in such

a way that offspring from different clutches could be discriminated through the analysis of body size and shape of the individual specimens. The clutch effect in this sense would comprise not only genetic but also phenotypic components such as incubation environment and maternal nutrition and sanitary status. Analogously, relatively isolated small populations could be discriminated by similar analysis. Although crocodilian growth rates are notoriously variable even within single populations, age estimation from growth curves can be useful for gross demographic analysis (Huttan 1987). Skeletochronology could be used for more detailed work, such as the study of age specific fecundity when post-mortem examination is feasible (Fergusen 1984).

Morphometric analysis and relative growth models are presented here as tools for the study of BSC clutches and population discrimination and individuals' body size, sex, and age assessment. Discriminating clutches and populations might help us to understand dispersal pattern and the colonization capacity of the species. Individuals' body size, age, and sex assessment -- even from preserved materials -- might help us to understand the structure of the target populations. The low cost and relative simplicity of morphometric analysis might corroborate it as a consistent set of alternative methods for the study of small populations.

CHAPTER 2
LITERATURE REVIEW

Morphometrics have been defined in different ways. The use of multivariate statistical analysis in morphometrics made Blackith and Reyment (1971) call it "Multivariate Morphometrics" and define this field as "the application of multivariate statistical analysis to biological variability in morphological characters". Oxnard (1978) widened this definition a little and called it the "characterization of biologically relevant forms and patterns in ways that allow their quantitative handling". In opposition to the multivariate statistical methods, a geometrical approach was brought to the arena by Bookstein (1982a) who defines morphometrics as the "empirical fusion of geometry with biology"..."the study of the geometrical form of organisms" (Bookstein 1986), or "the statistical study of biological shape and shape change" (Bookstein 1991). Complementarily to him, Rohlf (1990) defines this field as "the quantitative description, analysis, and interpretation of shape and shape variation". In response to the "geometrical school", Reyment (1991) restates that multivariate morphometrics is the "application of multivariate statistical analysis to biological variability in morphological characters, *and not only restricted to shape variation*" (italics added).

Lexicographically, morphometrics can be defined as "the measurement of external form of living organisms". The word derives from the Greek *morpho* (form) and *metrik* (metric). "Metric" can be defined as a standard of measurement, whereas the definition of "form" is less straightforward: "shape and structure of something", "external appearance of a body", "visible and measurable unit defined by a contour", or an "essential nature of a thing" (Merriam Webster Collegiate Dictionary 1996). More than defining the exact role of shape and shape variation and the best approach to its analysis, what seems to really intrigue morphometricians is the old question of how to describe the essence of the form of living organisms.

2 1 Historic Overview the Search for the Essence of the Form

The form of living organisms has been enchanting humans as both science and art since humans lived in caves and science and art were no more than vague and unlikely alternatives for their uncertain future Human s outstanding capacity of abstraction, the great variety of the form of living organisms forms or the simple necessity of recognizing their predators and preys made humans draw beasts on rocks, build up totems on villages hang up trophies on walls on an endless journey in search for the essence of the form of living organisms

Pythagoras of Samos believed that all things could be described by numbers, which means that their essences and structures could be determined by finding the numerical relations contained in them Essence of form was however the keyword for the *Ideas* or *Eidos* of Plato According to him all of the things that men perceive with their senses, including living organisms, appear to be imperfect copies of an ideal form like moving shadows on a wall Although keeping Plato s doctrine of purposiveness, Aristotle pointed out that all living beings develop from an imperfect to a perfect state after which they again decay and finally die having reproduced themselves (Weber 1925) The idea of a perfect essence of the living organism s form around which variation can be seen as mere imperfection lasted long enough to deeply influence the way humans classify living organisms

Linnaeus employed Aristotle s syllogisms to create his classification system Operating within a logical and theocentric framework he could *naturally* find species-specific *good* characters by which a species could be differentiated (Cain 1958 1958) Goethe embraced the idea that the essential form of an organism is related to its function In many ways he was a link between the dichotomic Linnean approach and the "gestalt" (whole organism) approach developed by Adanson (Wilkinson 1951)

The great variety of living organisms forms also seduced Charles Darwin However he did not see variation as imperfections of the ideal essence instead, he considered variation as the prime maker of evolution -- and consequently the origination of new forms -- by natural selection (Darwin 1859) Surprisingly evolutionary theory did not affect Linnean systematics more than superficially Form variation among species -- primarely taken for granted -- began to be seen as the result of the evolutionary process However the absence of quantitative information on the dichotomic systematics of Linnaeus led to the development of an alternative system the *Numerical Taxonomy* (Sokal and Sneath 1963 Sneath and Sokal 1973), which is still in dispute in taxonomic circles

Charles Darwin not only perceived the relationship between form and evolution but also between form and behavior of living organisms. For example, different feeding behavior would be related to different beak size and shape in birds. He also pointed out that sexual selection would be related to differences between the sexes both in terms of form (sexual dimorphism) and behavior (Darwin 1871).

The evolutionary approach has contributed significantly to the origin of a new insight into the study of behavior: a field called *Ethology*. Although not focussed on the relationships between form and behavior, the early *ethological* studies essentially reflected the idea that form and behavior would be the result of adaptation and evolution. The classical-conditioned dogs of Ivan Pavlov (1927), the bee-hunter wasps of Niko Tinbergen (1951), the hooded-chickens of Eckhard Hess (1956), the imprinted birds of Konrad Lorenz (1965), and the dancing bees of Karl von Frisch (1967), all showed an intrinsic morphological component associated with behavior.

Quoting the determinism of Sigmund Freud, "anatomy is destiny" (Freud 1965 [1914]). This would be such a concise but provocative bottom line for the relationship between form and behavior. Either a man or a wasp may change his destiny -- destiny not as an immutable fate, but something one intrinsically brings from the past that deeply influences one's future. As an analogy, the association between form and behavior would be like a stream. One could swim against or go with it.

However, analogies are just analogies and they can attractively lead us to false conclusions. This seems to have happened when some people on the 18th Century started believing that the shape of the human skull would be a strong indicator of their behavior. Even the prominent biologist Alfred R. Wallace (1899) was influenced by the belief that the conformation of the human skull was indicative of mental faculties and character: the study of which was then called *Phrenology*. Although remembered today as only a method of reading character from the contour of the skull, the ideas of Franz J. Gall, Johann G. Spurzheim and George Combe were self-designated as an experimental science with the a priori assumption that mental phenomena have natural causes which could be determined (Davies 1955).

From labelling individuals based on their skull shape to labelling races using similar criteria was a short step. Human cranial morphometry was used and abused to rank human races defending the superiority of whites over blacks and Indians in what was pseudo-scientifically called *Craniometry*, another numerical approach for biological determinism (Gould 1981). Comparing and creating different races of livestock based on isoteric criteria like ear size or fur color was not exactly unusual in England in the 19th Century. Although some of these criteria

had a numerical basis they still kept the *Idea* of the essence of the form as a standard of perfection

In his book *On Growth and Form*, D Arcy W Thompson (1917) introduced the idea that living organisms are shaped by physical constraints. His central argument was that surface/volume ratios must decline as organisms grow in size. Therefore, according to him, small creatures should be the product of surface forces whereas large creatures should be the product of gravitational (volumetric) forces. He used Cartesian coordinates to describe shape relationships between organisms. This could be called the *geometry of the essence* and its concepts still influence the way biologists deal with size and shape of living organisms

2.2 Contemporary Trends: the Uncertainty of Size and Shape

Cartesian coordinates, which are named after Decartes, are a system of positioning individual points in a two-dimensional plane based on their distance from two intersecting lines, called axes. Their use in the study of biological form transformation is often attributed to D'Arcy Thompson, but it dates from the Renaissance art (Bookstein 1993). Although D Arcy Thompson did not present mathematical calculations, his intuitive method of explaining shape transformation in living organisms as distortions of Cartesian coordinates is still considered classic by many biologists. Only decades later, from the late 1970's to the late 1980's, Thompson's transformation grids were quantified in a statistical way. Growth studies were primarily stimulated by his *On Growth and Form*, especially the concept of differential growth as elaborated by Huxley (1924 and 1932).

Huxley was possibly the first to systematically study differential growth rates. His basic supposition was that growth takes place at different rates in different directions and at different points. He analyzed many examples of the growth of specific organs in relation to the growth of the body. He described this relationship with a simple mathematical expression

$$Y = aX^b$$

where Y is the size or weight of the differentially growing organ, X is the size or weight of the animal (discounting the size or weight of the organ in question), and a and b are constants.

Although using a different approach than the geometric used by Thompson, Huxley also worked with size and shape transformation in living organisms. The relative growth of the organs studied was seldom the same as the animal's body. In other words, the proportion of the organs (or other parts of the body) in relation to the animal's body changed during the growth process

(1 n., the constant *b* was frequently different than one). For this reason, this mathematical expression was called as *allometric equation* (from the Greek *allo*- "different"), in opposition to the idea of an *isometric* (from the Greek *iso*- "uniform") growth where size varies, but shape does not.

Reeve and Huxley (1945) recognize that other authors have pointed out before that certain organs show a noticeable change of relative size with increase of body size. Pezard (1918) described it as *heterogenic* growth and Champy (1924) called it *dysharmonic* growth. However, these terms were unsatisfactory because of ambiguous or alternative meanings (Huxley and Teissier 1936). In addition, these studies were not quantitative analysis of differential growth as first presented by Huxley (1924, 1932).

The studies of Thompson and Huxley led to a great number of biological studies concerning size and shape transformations of living organisms. They still do. At that time, however, if the concept of *transformation* was not controversial (both evolutionists and creationists agreed that living organisms forms changed!), the concepts of shape and even size came out to be not exactly clear. Huxley used simple length measurements as body size, although he knew body size could be more related to volume or weight. Thompson, by his turn, proposed a more geometrical approach to the study of biological forms. However, living organisms do not fit well in triangles, circles, rectangles or squares. Therefore, the classic Euclidean Geometry could not be applied sufficiently to describe biological forms. This possibly was the reason that Thompson failed in proposing computational methods for your grid transformations. There were no computations available for this purpose at that time. Medawar (1945) and Richards and Kavanagh (1945) were possibly the first to try to accomplish them, not by coincidence in a book called *Growth and Form: Essays Presented to D'Arcy Thompson* (Le Gros Clark and Medawar 1945).

Medawar (1945) suggests four essential stages in the analytic procedure of shape transformations on humans as a function of age: "the treatment of each figure, and each set of measurements derived from it, as a separate analytic object; the defining of a transformation between each such figure and an arbitrary chosen initial figure by means of a single function with different parameter values; the reduction of the parameters to their efficient number; and the replacement of each parameter by a continuous function of a single variable parameter standing for time" (italics on the original). According to this procedure, each sector of the whole figure would be treated individually through the computation of a single variate. Richards and Kavanagh (1945) went further and proposed the utilization of (simple) geometric concepts like

length, area and volume on an attempt to incorporate the concept of allometric growth of Huxley on the transformation grids of Thompson.

The allometric equation developed by Huxley used only two variates at a time. This bivariate model could efficiently explain the relationship between the variables utilized, but not necessarily among other variables not included. Multivariate statistical analysis developed during the 1930's and 1940's (Fisher 1936, Mahalanobis 1936, Rao 1948) could be useful on the problem of biological classification through the calculation of (statistical) *distance* among (statistical) populations, based on biometric variables. This is what Penrose (1954) believed. He also believed that this statistical distance could be broken down into two parts: *size* and *shape*.

According to Penrose, the shape-distance would be related to the variation among differences between means values of any two populations (which he called *d* values), whereas size-distance would be related to the sum of the *d*-values of all characters studied. Thus, when the shape-distance between two objects or organisms was zero, they would just vary in terms of size, but not in terms of shape. Penrose incremented the way size and shape variation could be analyzed, but yet, he did not help to clarify their vague concepts.

The allometric relationships between organisms growth and physiological activities particularly metabolic rate as defined by oxygen consumption, was initially studied by Kleiber (1932, 1941, 1961) and developed extensively by McNab (1963, 1966, 1970, 1973) and others (Eisenberg 1980, Schmidt-Nielsen 1984). These studies linked the morphological effects of changing in body size to physiology and ecology.

Simpson, Roe and Lewontin (1960) studied the biological significance of the constants on the allometric equation of Huxley (*a* and *b*, above). They concluded that the body presents a general field of growth potential and that changes in proportions are the results of the varying intensities of this potential. They also suggest that the use of ratios instead of absolute dimensions would be more efficient to capture variations on the intensity of this growth potential. There is a clear, although not assumed, reference to the differentiation of size ("absolute dimensions") and shape ("proportions"), but they are not yet well defined. Only when Jolicoeur and Mosimann (1960) used principal components analysis on the study of size and shape variation in the painted turtle is that size and shape could be clearly put statistically apart.

The techniques of principal components analysis was first developed by Karl Pearson (1901). According to Manly (1994: 76), Pearson "apparently believed that this was the correct solution to some of the problems that were of interest to biometricians at that time, although he did not propose a practical method of calculation for more than two or three variables." The

statistical properties of principal components were described later by Hotelling (1933). A principal components analysis tries to explain the variance-covariance structure of a group of variables through a few uncorrelated linear combinations of them. Geometrically these linear combinations represent the selection of a new coordinate system obtained by rotating the original system (Johnson and Wichern 1992).

Using three biometric variables of painted turtle's carapace Jolicoeur and Mosimann (1960) found out that the first principal component corresponds to a variation of size (i.e., growth trade), whereas the second and third principal components correspond to a separate variation of the various characters (i.e., shape variation). In other words, if there is only size variation among individuals (i.e., if individuals are similar or if they keep the same shape during the growth process), there is only one principal component responding for the total variation, and all of its coefficients present the same signal. On the other hand, when there is also a shape variation other principal components result from the analysis, and they present positive and negative coefficients, which means that contrasts between biometric variables also contribute to the total amount of variance. Variance coming from the contrast between different sets of variates can be interpreted as a *residual* shape variation. Rao (1964) gives a mathematical justification for this argument.

This new approach seemed to be as interesting that Teissier (1968) and Jolicoeur (1963a) proposed a multivariate generalization of the allometric equation based on the first principal component coefficients. Teissier proposed the use of the correlation matrix of the log-transformed biometric data because it tends to make principal components independent from the order of magnitude and the scale of measurement of the variables. Correlation matrix is the covariance matrix for the standardized variables. Its use indeed reduces dimensionality of variation and it is appropriate when differences in variables scaling could mascarade total variance. Jolicoeur, however, advocated that logarithmic transformation generally carried out on relative growth data tends in itself to make the covariance matrix independent from magnitude and scaling. Thus, he proposed that the best manner to generalize the allometric equation is the first principal component of the covariance matrix of log-transformed biometric data. Hopkins (1966) and Sprent (1968) argued that this procedure was not completely satisfactory unless one took into account the nature of the remaining components, which seems to have been done by Jolicoeur (1963b) on a study of robustness in the North American marten (*Martes americana*). However, in spite of any small controversy, a significant step was done at that time: the study of biological relative growth earned a definitive multivariate approach.

A few years before Reyment (1960) had proposed a generalization of the allometric equation through the use of multiple linear regression but this procedure has some problems it does not eliminate the correlation among variables, it may be affected by the scaling of measurement, and it sets one variate apart from all the others (as a dependent variable or response) which prevents it from expressing the various possible allometric relationships between all pairs of variates.

The evolutionary, taxonomic, and physiological implications of allometric relations are extensively discussed by Stephen J Gould (1966) He redefines allometry in a broader sense not confined to any one form of mathematical expression such as the power function as the study of proportion changes correlated with variation in size of either the total organisms or the part under consideration He points out that variates may be morphological physiological or chemical and the size differences may appear in ontogeny phylogeny or the static comparison of related forms differing in size He also suggests the use of factor analysis on the multivariate generalization of allometric relations

Factor analysis is somewhat similar to principal components analysis It also describes a set of variables in terms of a small number of indices or factors and then helps to elucidate the covariance relationship between these variables however its statistical analyses are more elaborate (Manly 1994). Factor analysis was developed by Charles Spearman (1904) He studied the correlations between test scores of various types and noted that many observed correlations could be accounted for by a simple model for the scores which caused a considerable controversy when Spearman Karl Pearson and others used this procedure to define and measure *intelligence* (Johnson and Wichern 1992)

Although apparently successful on the separation of size and shape components or factors multivariate analyses were never successful in their definition This problem possibly could be solved if some consistent computation methods were developed for the transformation grids of Thompson This was what Sneath (1967) pursued He proposed the following steps for the comparison of two diagrams, coordinates of corresponding points are marked and diagrams are scaled in order to give the best possible fit. This would give measures of size and shape difference The displacement of each point and its correspondent on the other diagram are then analyzed in terms of linear quadratic cubic or higher trend surface analysis Correspondent points are called as homologous points, in the sense of the operational homology used by taxonomists (Sokal and Sneath 1963, Sneath and Sokal 1973) which does not mean that they descent from a common ancestor Although somewhat related to what was proposed by Medawar

(1945), this procedure was imported from geologists who developed trend surface analysis and computer programs to study the regional and local trends of contoured maps (Krumbein and Graybill 1965 and others cited by Sneath)

Although trend-surface analysis indeed improved the analysis of *pure* – i.e. size independent – shape, its basic limitation for the study of biological forms is that this procedure is restricted to individuals' shapes. This may sound reasonable for a geologist, for whom a single map of a certain area may be enough (geographic areas are unique!). However biologists generally work with populations of individuals which vary and therefore require sampling, which in its turn requires statistical analysis. Geometric analysis of individuals' shapes may be intellectually delightful but biologically innocuous, unless one is looking for sketches of typical organisms. This could be claimed by any biologist who worked with growth or any other kind of quantitative variation on the late 1960's and 1970's. However in a certain sense, taxonomists used to look for sketches of typical organisms before the late 1960's and they kept doing so during the 1970's.

The use of computers and statistical softwares stimulated the use of multivariate techniques on the study of living organisms forms, which at that time already could be called as *morphometrics* (Blackith 1965). Multivariate techniques seemed to efficiently explain variance among individuals and covariance among variables. These procedures also seemed to be efficient in showing size and shape components of biological transformation. However they did not present any information about the geometry of the species studied, which was exactly the strength of Thompson's transformation grids. Nonetheless, these were insufficient to handle statistical variation.

The first possible attempt to reconcile multivariate statistical analysis with the trend surface analysis was done by Oxnard (1969). He proposed the use of canonical axis on grid transformations, which seemed to have been more effective to stimulate the use of canonical analysis itself than its application on Thompson's grids. Canonical correlation analysis is efficient for identifying and quantifying the associations between two sets of variables. It was initially developed by Hotelling (1935, 1936) as an attempt to relate arithmetic speed and power to reading speed and power. Its possible ecological applications are extensively discussed by Gittins (1979). This technique reduces dimensionality between two sets of variables into a few pairs of canonical variables (Johnson and Wichern 1992). The idea of Oxnard was that this technique could efficiently clarify the relationships between size and shape variables.

Other attempts to mathematically define size and shape were stimulated by the idea of the multivariate generalization of the allometric equation. Mosimann (1970) defines shape as vectors of size variables and thus stated that shape is virtually always related to a variety of size variables. Gould (1971) states that the coefficient *a* of the allometric equation (see above) is not a size-independent difference between regressions as believed on the contrary it expresses differences in size between comparable animals of similar shape. He also suggests that when the coefficient *b* is invariant for two regressions a criterion of geometric similarity can be extracted from the two *a*-values.

The concept of geometric similarity introduced by Gould would considerably influence future comparative studies between different organisms, although not exactly the way he proposed i.e. not restricted to the bivariate allometric equation. When a biologist asks how similar two organisms are the idea of intermediary (or *in between*) forms is implicit. Intermediary forms can carry the utmost important information on evolution, physiology and other fields of biology. Increasing the number of variates, one would increase the dimensionality for comparison between different forms. Once again multivariate statistical analysis would be *the* way to see how different (or how similar!) two or more living forms really are. The prefix *Multivariate* was then added to the blooming field of *Morphometrics* (Blackith & Reyment 1971).

Initially Blackith (1965) describes morphometrics as a synonym of numerical taxonomy "a quantitative approach to taxonomic derived from the Pythagora s view that in numerical relations lay the essence of taxonomy". Later however Blackith and Reyment (1971) suggest that numerical taxonomy and morphometrics could be considered as diverging branches of the same field, possibly denominated "quantitative taxonomy". In addition they suggest that "another approach is to regard all these topics as branches of morphometrics and to describe multivariate changes of shape and size as falling into the province of *discriminatory topology* (italics added), since many of the techniques are based, directly or indirectly on the discriminant function" (Blackith and Reyment 1971:272).

They referred to the discriminant function analysis initially developed by Fisher (1936) to separate individual observations from two or more known populations. Considering that this group of techniques are not restricted to interspecific morphological variation (the basic interest of taxonomists), but also to intraspecific variation (e.g. sexual dimorphism, ontogeny and many others). Blackith and Reyment were not wrong. The problem is that apparently they did not separate adequately the technique from the field. For biologists (including taxonomists),

multivariate statistical analysis is a set of techniques that can be used to help them to better understand biological processes that affect shape and size of living organisms. For a taxonomist interested in a specific group of invertebrates as much as for a wildlife biologist interested in the sexual dimorphism of hatchling alligators. Paradoxically, this was probably the major contribution of their book *Multivariate Morphometrics*: the detailed description of the most useful multivariate statistical analysis, even better described in the second edition thirteen years later (Reyment, Blackith, and Campbell 1984).

Blackith and Reyment considered size and shape as components of the form of living organisms whose transformations could be explained by principal components analysis as proposed by Jolicoeur and Mosimann (1960). They were actually skeptical to relation to the use of outlines as shape descriptors. They even noticed that through the use of trend-surface analysis of transformation grids "quite simple deformations will convert the outline of a rabbit into that of a rhinoceros, as Thompson showed" (Blackith and Reyment 1971: 326). However, not all biologists agreed with them. For instance, for a palynologist interested in taxonomy, not much more than the contour of a pollen grain can be easily seen, and therefore used to identify species. In this case, the outline of the pollen itself could be *the* difference between species.

As an example of the above, Christopher and Water (1974) proposed the use of Fourier series to quantitatively describe miospore shape. Fourier series (also called "Fourier analysis" or "harmonic analysis") is a mathematical expression of sine and cosine waves which can be useful to round and describe outlines. Its mathematical steps and procedures are commonly described in engineering mathematics texts (e.g., Pipes 1946 and others cited by Christopher and Water). Other attempts to promote the use of Fourier analysis or one of its variants were possibly stimulated by the development of new methods of computerized image acquisition (Rohlf and Archie 1984 and Ferson *et al.*, 1985).

However, there was something missing on the concept of shape as just the outline of an organism and mainly on the concept that multivariate statistics could efficiently describe the *geometry* of shape (Humphries *et al.* 1981). According to Fred Bookstein (1978) it did not. According to him both concepts lack the idea of *landmarks*: anatomical structures used as points of orientation in locating other structures (for his specific critique on the use of Fourier analysis see Bookstein *et al.*, 1982). The implications of this simple concept revolutionized the field of morphometrics in no more than a decade.

According to Bookstein (1977a) shape and shape change should not be treated by discrete variables, vectors of preset distance-ratios or other equiform invariants, as it used to be

by multivariate statistical analyses. Instead, according to him, shape measurements should be functional in order to provide geometric information about organisms' form. He assumed that this was exactly what D'Arcy Thompson proposed in 1917. However, he was concerned that D'Arcy Thompson did not develop a mathematical framework for this (Bookstein 1977b). He gave himself this mission, and his first attempt was to represent Thompson transformations by what he called *biorthogonal grids* (Bookstein 1977a).

Biorthogonal grids would remain orthogonal even after transformation, contrary to Thompson's grids. These grids directly generalized the forms of classic growth gradient analyses in the context of two-dimensional Euclidean and Riemannian geometry. Shape change would be represented as a symetric tensor field upon every point of an organ or organism, which means that shape change could be reduced geometrically to differential change in size (Bookstein 1978).

However, although biorthogonal grids "provided shape comparisons in a canonical coordinate system", this method "was not consistent with visualizations of standard error or any other notion of sampling variance for the features displayed" (Bookstein 1993: 25). In other words, this method was efficient to represent individual shape change, but it did not deal efficiently with variation among individuals in a statistical way. His first attempts to solve this problem were the use of triangles (Bookstein 1982a,b, 1984a,b, 1985) and truss measures (Strauss and Bookstein 1982, Bookstein *et al.* 1985) to describe shape and shape change. However, according to him, these methods were not able to solve statistical problems concerning distribution theory (Bookstein 1993: 26).

According to Bookstein, only when landmark locations were taken as raw data themselves, it was possible to apply full statistical analyses to geometrical studies of biological shape, in which he called "morphometric synthesis" (Bookstein 1993). Goodall (1983) derived the equivalent F ratio without using size standardizations. Taking the appropriate simplest case, Bookstein (1984b) introduced the shape coordinates for triangles and showed how shape differences can be weighed by Hotelling test T^2. Complementarily to them, Kendall (1984) announced the global shape spaces to which Goodall's and Bookstein's methods inadvertently applied as statistical metrics in tangent spaces. Their further publications (Bookstein 1986, Kendall 1989, Goodall 1991) reinforced the convergence of these three approaches on a single foundation for the study of landmark data.

As a step further, Bookstein (1989a) proposed the use of *thin-plate spline* functions for landmark data to fit the differences in the positions of landmarks in one organism relative to their positions in another. The name thin-plate spline carries an analogy with a spline that is fit to a

shape like an extremely thin metal plate over an object where the variance could be quantified via its "bending energy" (another analogy) The spline maps would be composed by linear parts, called *principal warps* "which are geometrically independent, affine-free deformations of progressively smaller geometrical scales" according to his creator

After this, there was a significant development of new methods and software programs with a strongly geometric approach for morphometric studies (Rohlf and Bookstein 1990 Bookstein 1991 Marcus *et al* 1993) Multivariate morphometrics became "traditional morphometrics" (Marcus 1993), in reference to the "new morphometrics" (Rohlf and Marcus 1993) or "geometric morphometrics" (Lynch *et al*, 1996). Data acquisition became considerably more sophisticated than the old-fashioned caliper (Becerra *et al*., 1993) and a considerable familiarity with geometry became a must to understand all the new jargons (Reyment 1991)

According to Reyment (1991), one should not feel too inadequate if one is having trouble with geometric morphometrics because "no matter how much experience you have in multivariate statistical applications you will most likely find geometric morphometrics heavy going the first time you encounter it, and even the second time and perhaps the third time" According to him, the possible reason for that is the unfamiliarity of these new ideas and the mathematical methods even for professional statisticians.

Behind this argument, there is still the same controversy about how to define the shape of living organisms The so-called geometric morphometricians claim that the so-called multivariate ("traditional") morphometrics lead (at best) to path diagrams, not to sketches of typical organisms (Bookstein 1993 19), with impressive definitions of "size and shape" (Bookstein 1989b) However even the simplest geometrical shape – a triangle – can be extremely difficult to be defined by an experienced mathematician with solid background in Physics (see Watson 1988) A simple drop of water hanging from a faucet, before breaking off assumes a three dimensional shape so complex that the calculation of the shape alone, according to Robert Shaw (1984) -- a physicist specialist in chaos -- is a "state-of-the-art computer calculation" (Gleick 1988)

Geometric morphometrics is based in two principles. landmarks and outlines (Reyment 1991) However, the exact geometric limits of both depend on their image scale Approaching more and more to any shape contour (assuming a theoretical infinite capacity to do so), it would be possible to see that discontinuity is always present A good analogy for this was developed by Benoit Mandelbrot (1977) when he asked himself and others "how long is the coast of Britain" and ended up developing what is called *Fractal Geometry* According to Mandelbrot, the answer

for this question depends on the scale of the map or (adding some complexity) how many dimensions it includes. According to Gleick (1988) "Mandelbrot found that as the scale of measurements becomes smaller the measured length of a coastline rises without limit, bays and peninsulas revealing ever smaller subbays and subpeninsulas at last down to atomic scales, where the process does finally come to an end. Perhaps." In their effort to improve sketchy representations of biological shape, geometric morphometricians migrated from classic Euclidean to Reimmanian Geometry but there is no sign yet that they have arrived in Fractal Geometry.

Geometric models are usually far more complex than multivariate ones. However, it does not mean that they capture all nuances of living organisms' size and shape in what has once being called the essence of the form. Models and sketches are useful and attractive because they help people to *see* what they have difficulty to *visualize* (Abercrombie and Verdaasdonk 1995). However, even the best "sketch of a typical organism" is just a sketch, which by definition must be simpler than the real organism. Otherwise, it would be much wiser to use the real organism itself. Being *simple* means being an approximation of reality as simple as possible, as complex as necessary. Multivariate morphometrics models can be simple enough to understand the basis of morphological variation and complex enough to permit an efficient discrimination of different groups or categories of organisms. This is the general goal of the present study.

CHAPTER 3
MATERIALS AND METHODS

The present study aims at the development of morphometric models that can be useful for the assessment of the following BSC individual characteristics: *clutch size*, *age*, *area of origin* and *environment* (captive or wild). For this purpose, body and head measurements were taken from 244 captive and 25 wild animals.

3.1 Study Sites

The captive animals were located at *Escola Superior de Agricultura "Luiz de Queiroz"*, University of São Paulo, Piracicaba, State of São Paulo, Brazil. Information about their age, sex, date of birth, and pedigree are available on the Brazilian regional studbook of the species (Verdade and Santiago 1991, Verdade and Molina 1993, Verdade and Kassouf Perina 1993, and Verdade and Sarkis, in press). The wild animals were captured on small wetlands associated with tributaries of Tiete River in East-Central São Paulo State (Figure 1, Table 1).

Morphometric differences between wild and captive animals are evaluated in order to understand how exactly the captive environment influences animals morphology. A similar study is being conducted by Meers (1996) with the American alligator, wherein he expresses his concerns that the captive environment could be detrimental to crocodilians in reintroduction and conservation programs.

3.2 Field Techniques

Field studies were carried out from October 1995 to May 1996. Capture techniques consisted of approaching the animals by boat at night with a spotlight. Juveniles (<1.0 m total length) were captured by hand, similar to the method described by Walsh (1987). Noosing, as described by Chabreck (1963), was tried unsuccessfully for adults. The adult caimans were too wary and usually submerged before the noose was in place, similar to what was experienced by Webb and Messel (1977) with *Crocodylus porosus* in Australia and Hutton *et al.* (1987) in

Zimbabwe Rope traps (adapted from Walsh 1987) were also tried unsuccesfully for both adults and young. Captive non hatchlings were taken either by hand or noose according to their size on daytime in October 1996. One day old hatchlings were measured in March April 1996.

The captured animals were physically restrained during data collection. No chemical immobilization was used. Body measurements (body size variables) were taken with a tape measure (1 mm precision). Head measurements (head size variables) were taken with a steel Summit Vernier caliper (.02 mm precision, second decimal disconsidered). Body mass was taken with Pesola hanging scales (300 x 1g, 1000 x 2g, 5000 x 5g, 20 x 0.1 kg, 50 x 0.1 Kg, depending on individual body mass). Eggs were measured with the same caliper described above. Egg mass was taken with a Filmola 200 electronic scale (.01 g precision, second decimal disconsidered). Before final measurements were taken training sessions were carried out and measurements were repeated until variation between observers were negligible, i.e. less than the desired precision. Animals were sexed through manual probing of the cloaca (Chabreck 1963) and/or visual examination of genital morphology (Allstead and Lang 1995) with a speculum of appropriate size.

3.3 Subjects and Variables

Four body-size, fourteen head-size and eleven ratio variables were taken from wild and captive animals. Morphometric models were developed in order to assess individual's body length, sex, age, clutch of origin, area of origin, and environment (wild or captive). Eight head-size variables are "length" measurements in the sense that they are longitudinal in relation to the body. The other six head-size variables are "width" measurements in the sense that they are transversal in relation to the body. Ten head size variables are located on the upper jaw and cranium, whereas the other four head size variables are located on the lower jaw. Five ratio variables represent relative "length", whereas the other six represent relative "width". Eight ratio variables are located on the upper jaw and cranium, whereas the other three are located on the lower jaw (Figure 2, Table 2).

One of these measurements, PXS, the length of the premaxillary symphysis, is not visible in live animals but is closely approximated by the distance from the snout tip to the anterior tip of the first tooth posterior to the prominent groove in the snout behind the nares (usually the 6th or 7th tooth).

Figure 1 Partial distribution of BSC in southeast South-America (shaded area). It includes the whole State of São Paulo (black area) and the area wherein wild animals were captured for the present study. Adapted from Thorbjarnarson (1992).

Table 1 Study sites description. Apparent population size: maximum number of animals seen during night-counts. Sample size: number of animals captured.

A. Volta Grande	
Watercourse associated	Piracicaba River
Latitude	22°40'41" S
Longitude	47°55'21"W
Area (ha)	≈ 80
Habitat type	*varzea* (wetland)
Common aquatic plants	Fam. Cyperaceae: *Cyperus* sp.
	Fam. Haloragaceae: *Myriophyllum brasiliensis*
	Fam. Pontederiaceae: *Pontederia* sp. 1
	Fam. Salviniaceae: *Salvinia rotundifolia* and *S. auriculata*
Apparent population size	9
Sample size	2

B. Porto de Areia	
Watercourse associated	Piracicaba River
Latitude	22°39'02"S
Longitude	47°58'52"W
Area (ha)	≈ 200
Habitat type	lagoon
Common aquatic plants	Fam. Pontederiaceae: *Eichornia crassipes* and *E. azurea*
	Fam. Thyphaceae: *Typha angustifolia*
	Fam. Lentibulariaceae: *Utricularia* sp. 1
	Fam. Nymphaeaceae: *Nymphaea* sp. 1 and sp.2
	Fam. Hydrocharitaceae: *Eloden densa*
	Fam. Salviniaceae: *Salvinia auriculata* and *S. rotundifolia*
Apparent population size	21
Sample size	9

Table 1 (cont.) Study sites description. Apparent population size: maximum number of animals seen during night-counts. Sample size: number of animals captured.

C. Pantanal	
Watercourse associated	Aracna Creek
Latitude	22°35' 58"S
Longitude	47°51' 51"W
Area (ha)	≈ 10
Habitat type	lagoon
Common aquatic plants	Fam. Typhaceae: *Typha angustifolia*
	Fam. Haloragaceae: *Myriophyllium brasiliensis*
	Fam. Pontederiaceae: *Pontederia* sp.2
	Fam. Nymphaeaceae: *Nymphaea* sp.3
Apparent population size.	22
Sample size.	3

D. Charqueada	
Watercourse associated	Aracna Creek
Latitude	22°30'24"S
Long tude	47°49'29"W
Area (ha)	≈ 2
Habitat type	*açude* (artificial pond)
Common aquatic plants	Fam. Typhaceae: *Typha angustifolia*
	Fam. Cyperaceae: *Eleocharis* sp
	Fam. *Poaceae* sp 1
	Fam. Nymphaeaceae: *Nymphaea* sp 4
Apparent popyulation size	6
Sample size	3

E. Dourados	
Watercourse associated	Pederneiras Creek
Latitude	22°26' 32" S
Longitude	48°52' 22" W
Area (ha)	≈ 5
Habitat type	*açude* (artificial pond)
Common aquatic plants	Fam. Haloragaceae: *Myriophyllium brasiliensis*
	Fam. Lentibulariaceae: *Utricularia* sp.2
	Fam. unknown: Algae
	Fam. Poaceae: sp 2
	Fam. Cyperaceae: *Cyperus* sp. and *C. brevifolius*
Apparent population size	29
Sample size.	12

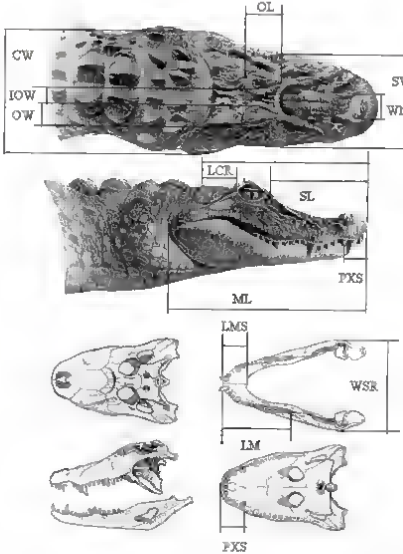


Figure 2. Morphometric variables. Dorsal and lateral view of *Caiman latirostris* head. See Table 1 for description of variables. Adapted from Wermuth and Mertens (1961:351, Fig. 250, after Natterer 1840 *Ann. mat. hist.* Wien 2: Tab. XXII)

Table 2 Morphometric variables (adapted from Jordansky 1973 and Holl and Portter 1994) and other symbols used in this study

Abbreviation	Type	Explanation	Unit
SVL	Body size	Snout vent length	cm
TTL	Body-size	Total length, anterior tip of snout to posterior tip of tail	cm
BW	Body-size	Commerc al belly width the width across the ventral belly and lateral flank scales between the distal margins of the third transverse row of dorsal scales	mm
BM	Body-size	Body mass	Kg*
DCL	Head-size	Dorsal cranial length, anter or tip of snout to posterior surface of occipital condyle	mm
CW	Head-size	Cranial width distance between the lateral surfaces of the mandibular condyles of the quadrates	mm
SL	Head size	Snout length anterior tip of snout to anterior orbital border measured d egonally	mm
SW	Head-size	Basal snout width width across anterior orbital borders	mm
OL	Head-size	Maximal orbital length	mm
OW	Head-size	Maximal orbital width	mm
IOW	Head size	Maximal interorbital width	mm
LCR	Head-size	Length of the posterbital cranial roof distance from the posterior orbital border to the posterolateral margin of the squamosal	mm
WN	Head-size	Maximal width of external nares	mm
PXS	Head-size	Length of palatal premaxillary symphysis (approximated for live animals by the distance from the anterior tip of snout to anterior tip of the first tooth posterior to the premaxial grove in the snout behind the nares (usually the 6th or 7th tooth)	mm
ML	Head-size	Mandible length anterior tip of dentary to the posterior tip of the retroarticular process	mm
LMS	Head-size	Length of the mandibular symphysis	mm
WSR	Head-size	Surangular width posterolateral width across surangulars at point of jaw articulation	mm
LM	Head-size	Length of lower ramus anterior tip of dentary to posterior margin of distal most dentary alveolus	mm
RCW	Head-shape	Relative cranial width CW/DCL	
RLST	Ratio	Relative length of snout SL/DCL	
RWST	Ratio	Relative width of snout SW/SL	
ROL	Ratio	Relative orbital length OL/DCL	
ROW	Ratio	Relative orbital width OW/OL	
RWI	Ratio	Relative interorbital width IOW/OL	
RWN	Ratio	Relative width of external nares WN/(DCL-SL)	
RPXS	Ratio	Relative length of premaxillary symphysis PXS/DCL	
RLSS	Ratio	Relative length of mandibular symphysis LMS/ML	
RWM	Ratio	Relative width of mandible WSR/ML	
RLLMR	Ratio	Relative length of lower ramus LM/ML	
CL5	Animal ID	Reproductive female (clutches are identified by female ID)	
CL9	Animal ID	Reproductive female (clutches are identified by female ID)	
CL10	Animal ID	Reproductive female (clutches are identified by female ID)	
CL13	Animal ID	Reproductive female (clutches are identified by female ID)	
CL25	Animal ID	Reproductive female (clutches are identified by female ID)	
CL53	Animal ID	Reproductive female (clutches are identified by female ID)	
CL1	Animal ID	Reproductive male	
CL30	Animal ID	Reproductive male	
CL203	Animal ID	Reproductive male	

* BM unit for hatchlings g

The morphometric variables used in this study were adapted from Iordansky (1973) and Hall and Portier (1994). They are based on linear distances between landmarks (body and head size variables) or ratios between measurements (ratio variables). Hall and Portier call these ratios *relative growth indices*. Relative growth represents change of proportions as body size increases. The study of relative growth has been characterized by Gould (1966) as the study of size and its implications in ontogeny and phylogeny. However, disregarding growth processes and size implications, these ratios express non-metric shape variables in the sense that they represent relative length and width instead of absolute values.

The use of ratios present several disadvantages (Sokal and Rohlf 1995). According to them, ratios tend to be relatively inaccurate, not normally distributed, and discontinuous. However, since ratios are still used by some authors (e.g. Hall and Portier 1994) they have been included and discussed in the present study for comparative purposes.

3.4 Exploratory Analysis

Growth curves were created for one through ten year-old captive animals for all size and ratio variables. Univariate and multivariate discriminant analysis and body and head size and ratio variables are compared as age predictors. Age of wild animals are estimated based on morphometric methods developed for captive animals of known age.

Allometric relations between morphometric variables and body size were determined. These relations may have a useful application on the estimate of body size based on parts of the body (for examples concerning crocodilians, see Webb and Messel 1978 and Magnusson 1983). Allometric relations of reproduction were also determined in order to investigate the female investment on clutch mass (Reiss 1989).

3.5 Methodology

Three consecutive questions are tested on the present study, concerning the following dependent variables: *clutch*, *sex*, *age*, *area of origin*, and *environment* (captive or wild) of individuals (Figure 3). The first and simplest one can be stated as: Is there a significant morphometric variation between groups i.e. between hatchlings from different clutches, between males and females, and between animals from different ages, areas of origin or environment? In other words, do animals from different groups vary morphometrically? Or yet, are the mean vectors of these statistical populations equal (Atchley and Bryant 1975)? In order to

answer these questions multivariate analyses of variance (MANOVA) were run taking clutch sex, age, site of origin and environment (captive or wild) as responses (dependent variables) and head size and ratio variables as models (independent variables)

The basic difference between (univariate) Analysis of Variance (ANOVA) and MANOVA is that for the first, an individual observation consists of only one single value or number whereas for the second an individual is represented by a set of values, each one corresponding to a specific variate In other words, in MANOVA and other kinds of multivariate statistical analyses, an individual can be represented as a matrix of one line and as many columns as variables in the model In ANOVA, an individual can be seen as a matrix of one and only line and one and only column The steps for MANOVA and ANOVA are similar However whereas ANOVA uses simple numerical algebra, MANOVA and other multivariate statistical analyses use matrix algebra, whose operations, although essentially the same, are more complex and time consuming than their numerical counterparts

If growth affects form differently in the groups above i.e., the answer for the questions above is positive a second question can be stated as Can the group to which a specific individual belongs be predicted? In order to answer this question discriminant analyses were run taking the groups above as response (dependent variables) and head size and ratio variables as predictors (independent variables)

The main purpose of discriminant analysis is to find linear combinations of the variables that maximize differences among pre-existing statistical populations (Atchley and Bryant 1975) Cross-validation is used to compensate for an optimistic apparent error rate which is the proportion of misclassified observations Apparent error rate tends to be optimistic because the data being classified are the same data used to build the classification function This procedure omits the first observation from the data set, develops a classification function using the remaining observations, then classifies the omitted observation. Next, it returns the first observation to the data set, omits the second observation and repeats the same process It continues in this manner with all observations in the data set (Minitab 1996) This process is similar to a jackknife procedure (Miller 1974)

The results of the linear discriminant analyses presented in this study include the classification matrix (also called "confusion matrix") and the linear discriminant functions (Minitab 1996) The squared distance (d^2) of a specific observation (x) to the centroid (mean) of a group (i) is given by the general formula below with the assumption of equal within group covariances

$$d^2(\mathbf{x}) = (\mathbf{x} - \mathbf{m}) \; S_p \; (\mathbf{x} - \mathbf{m}_i)$$

where:

$\mathbf{x}$ is a line vector of length p containing the values of the predictors for the observation

$\mathbf{m}_i$ is a column vector of length p containing the means of the predictors calculated from the data in group i

S_p is the covariance matrix calculated from the data in group i

An observation $\mathbf{x}$ is classified into group i if the squared distance of $\mathbf{x}$ to group i is the smallest. Thus, the formula above expands to

$$d^2(\mathbf{x}) = 2[\mathbf{m}_i \; S_p \; \mathbf{x} - 0.5 \; \mathbf{m}_i \; S_p \; \mathbf{m}_i'] + \mathbf{x} \; S_p \; \mathbf{x}$$

where the term in square brackets is a linear function of x, and is called the linear discriminant function for group i. For a given x, the group with the smallest squared distance has the largest linear discriminant function. Thus, this permits the classification of new observations (Mimiah 1996)

Principal components analysis (PCA) were run from correlation matrix of head-size variables and from covariance matrix of log-transformed size and ratio variables. Correlation matrix is the covariance matrix for the standardized variables. Its use reduces dimensionality of variation and it is appropriate when differences in variables' scaling could muscarade total variance. PCA rotates a correlation matrix, reducing correlation among variables to zero. Analogously, PCA rotates a covariance matrix reducing covariance among variables to zero. In both cases, however, variance is preserved (Manly 1994)

The results of the principal components analyses presented in this study are the eingenvalues (i.e. the variance of the principal components) the proportion and cumulative proportion of the total variance explained by each principal component, and the coefficients for each principal component. These coefficients are unique (except for a sign change on all coefficients) if the eigenvalues are distinct and not zero. If an eigenvalue is repeated, then the "space spanned" by all the principal component vectors corresponding to the same eigenvalue is unique, but the individual vectors are not. Therefore, the coefficients that one statistical package presents may not agree with the coefficients presented by another (Mimiah 1996)

PCA reduces dimensionality and helps interpretation of data often revealing relationships among variables that were not previously suspected (Johnson and Wichern 1992). Size and shape elements can be identified in PCA (Jolicoeur and Mosimann 1960). The first principal component corresponds to size variation, although log-transformation of data may result on the input of some shape variation on it (Hopkins 1966, Somers 1986). In other words, if there is only

size variation among individuals -- i.e., they are similar (sensu Thompson 1917) -- there will be only one principal component of natransformed data accounting for the total variation. On the other hand, when there is also a residual shape variation, other principal components result from the analysis (Dodson 1975).

At last, if it is possible to efficiently predict the group to which an individual belongs using *all* variables, it is worth determining which *subset* of variables are the most important source of variation for the model. The answer for this question is more vague than for the questions above, but not less important considering the time involved on measurements. In addition, it is usually desirable to work with as few variables as possible without significantly loosing efficiency. Some steps should be taken in order to answer this question. The first step in order to reduce the number of variables used in the present study was a best subset regression (Minitab 1996) where the "best subset" was chosen based on the highest coefficient of regression (r^2) for an arbitrary number of variables. Variable selection in this method is based on the fact that the subset model *may* actually estimate the regression coefficient and predict future responses with smaller variance than the full model using all predictors (Hocking 1976).

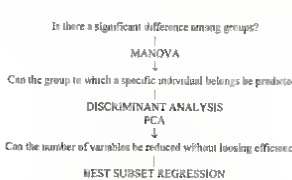


Figure 3. Questions and statistical procedures of the present study.

Caution is necessary when using an *automatic* procedure of variable selection because the solution from a purely statistical point of view may not be the best from a substantive perspective (Cody and Smith 1987). However, if -- as in this case -- the study purpose is to automatically distinguish statistical populations, it practically does not matter whether or not the

variables make biological sense (Rohlf 1990). After reducing the number of variables MANOVA discriminant analysis with cross-validation and PCA were repeated with the best subset in order to evaluate its efficiency.

Unless stated otherwise, log transformed size variables and ratios are separately analyzed for comparative purposes with their untransformed counterparts. Logarithmic transformation is a simple device that may ease and improve diagrammatic and statistical description of the effect of body size on other attributes (Peters 1983). Its utility in future studies is presented and discussed. All statistical analyses were done in Minitab for Windows (Minitab 1996) and their procedures are shown where adequate.

4.1 Variables: Distribution, Correlation, and Similarity

Descriptive statistics of all variables are presented in Appendix A. The majority of the variables are either normally distributed or present a distribution close to normal. Ratio variables tend to be not normally distributed and may lead to spurious correlations (Atchley 1978; Atchley *et al.* 1976) but these deleterious effects of the use of ratios did not significantly occur in the present study. Probability distributions of variables was assessed by Ryan-Joiner goodness-of-fit test (Ryan and Joiner 1976), which is similar to Shapiro-Wilk Test (Shapiro and Wilk 1965). The results are presented at Appendix A.

Although the captive neo-hatchlings sample distribution is skewed to young animals, the relatively large sample size (N=104 individuals), including 19 animals 5 year old or older counterbalances as much as it is practically possible the skewness deleterious effects. For age estimation animals were grouped by age, from one to five years old. In this case, distribution was normal or approximately normal for virtually all morphometric variables in all considered age classes.

On the growth curves and on the allometric studies of captive animals (items 4.2.1 and 4.2.3 respectively) underrepresented size- or age-classes could influence regression equations as outliers. This is a common problem with any biometric application of regression equations (for discussion see Peters 1983: 21-23). A visual examination on figures 5 - 6 suggests that this problem may be happening on the growth curves of captive animals. The absence of animals six and eight years old and the presence of a "big" seven-year old and a "small" nine-year old single individuals may erroneously suggest that the whole population would tend to decrease in body size from seven to nine years of age. Mathematically speaking, this could lead us to represent the growth curve of these animals with a cubic instead of a linear or quadratic equation--as presented on Table 4 and discussed later on item 4.2.1.

Captive neo-hatchlings are female biased whereas wild animals are male biased. This may have had some influence on the results of the studies of differences between wild and

captive animals, as presented and discussed later on item 4.4.2. Gender is also based through age classes of captive animals. This may have had some influence on the results of the sexual dimorphism study of captive animals, as presented and discussed later on item 4.2.4.2.

A correlation matrix is presented on Appendix B. Body- and head-size variables are highly correlated in wild and captive non hatchling animals. Correlation coefficients varied from 0.792 to 0.989 in wild animals and from 0.891 to 0.997 in captive non hatchlings. Hatchlings presented a considerably lower correlation between body- and head-size variables, varying in absolute values from 0.006 to 0.939. Correlation coefficients among ratio variables and between them and head-size variables were in general considerably lower, varying in absolute values from 0.033 to 0.743 in wild animals, and from 0.011 to 0.915 in captive non hatchlings. Similarly to the pattern described above, hatchlings presented a considerably lower correlation among ratio variables and between them and head size variables, varying in absolute values from 0.011 to 0.832.

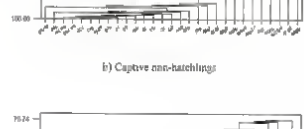
The present study is exploratory in the sense that one of its goals is the determination of which set of morphometric variables are more affected by clutch, gender, growth, age, area of origin and environment. A practical significance of these high correlation levels among variables for future morphometric studies is that most of them can be inferred from each other. Consequently, it is possibly not necessary to take them all every time, which would be time-consuming. However, in some circumstances, if independent variables are correlated, then the partial regression coefficients associated with them may not be assumed to reflect the dependence of one on another that exists on the population. This correlation among independent variables is known as *multicollinearity*, *non-orthogonality* or *ill-conditioning among variables*. In practice this is of little consequence if it is slight, but, if multicollinearity is substantial then consequences can be spurious (Zar 1996:419). In the present study those high correlation coefficients were determined for some of the dependent variables only (head- and body-size variables). No consistent multicollinearity was detected for independent variables (clutch, sex, age, site of origin, and environment).

Clustering of variables based on similarity levels can be helpful to classify variables into groups, when the groups are initially not known. Agglomerative clustering begins with all variables separate, each forming its own cluster. In the first step, the two variables closest together are joined. In the next step, either a third variable joins the first two, or two other variables join together into a different cluster. Each step results in one less cluster than the step before until, at the end, all variables are combined in one cluster. Once two variables are

combined as a cluster they may join with other variables but they will always remain together (Figure 4)

a) Wild animals

b) Captive non-hatchlings



c) Captive hatchlings

Figure 4 Agglomerative hierarchical clustering of variables (Minitab procedure. Stat → Multivariate → Cluster Variable)

Body and head size variables are clustered apart for both wild and captive non-hatchling animals whereas this pattern is not followed for hatchlings Hatchlings present most of their ratio variables clustered together with their related head-size variables Thus SL and RLST are clustered together the same happening with WN and RWN LM and RLLMR, LMS and RLSS IOW and RWI and PXS and RPXS This difference between hatchlings and older animals is possibly caused by hatchlings smaller variance in body-size

In hatchlings the relationships between morphometric variables tend to be independent of body size This pattern is related to the lower correlation between variables shown by hatchlings since correlation was used to measure distance between clusters Correlation and similarity between variables and the influence of body size on the relationship between morphometric variables is discussed later with the allometric relations presented on item 4 2 3

4.2 Relative Growth

4.2 1 Growth Curves of Captive Animals

There are three general approaches to the analysis of growth data. One approach involves measurements that are independent observations or that can be treated as such Other statistical approaches are required if the same individuals are measured repeatedly over time The third approach is to fit growth data to models that assume particular functional relationships between size and time (Andrews 1982). The first approach above is used in the present study Growth curves are presented here as regression equations with age being the independent variable (X axis) and generally a single measurement related to body size (e.g., body mass or snout vent length) being the dependent variable (Y-axis)

Growth models have been developed in order to provide mathematical treatment to the process of biological growth "Von Bertalanffy s mechanistic growth model" (Bertalanffy 1938) and "Richards family of growth models" (Richards 1959) are the most utilized Richard's family includes von Bertalanffy and the following other widely used models as special cases. monomolecular, logistic or autocatalytic and Gompertz. The basic elements that differentiate these models are the growth rate and the point of inflexion of the curve (Brown and Rothery 1993)

No attempt is made in the present study to fit growth curves of captive animals in any growth model basically because the animals utilized were born and raised in captivity and their growth curves are of little utility to studying wild populations Polynomial regressions are presented as exploratory data for future studies only No extrapolation or generalization of such

equations beyond in hand data is proposed, which could be considered an "intellectual suicide quotting Abercrombie (1996) However the relatively large sample size and the availability of animals from a broad age spectrum (from one to ten years old) may be useful for preliminary analysis of growth pattern for the species.

Although usually studied separately, cell, individual, and population growth are essentially distinct parts of the same ecological process An individual can be seen as a population of cells that individually grow and die on a very complex system resulting in the growth of the individual as a whole In its turn the major events of an individual s growth environ – birth, maturity, and death – are intrinsically linked to the major causes of a population fluctuation While birth and death rates respectively for increase and decrease in the population size, individual maturity is deeply related to dispersal and reproduction which in turn accounts for the population and meta-population dynamics and on a last instance for the geographic distribution of the species

Von Bertalanffy noted the tremendous difficulty in mathematically modeling organism growth. He emphasized that growth is widely dependent on external factors such as nutrition, temperature, life space, as well as internal factors such as hormones, progressive differentiation, change of water content, and age (Bertalanffy 1938) He emphasized however examples from physics and physiology in which complex phenomena can sometimes be described by statistical laws and suggested that such procedures could apply to organic growth In the present study age and sex are presented and discussed as sources of variation for the growth of individuals Later in this study the influence of other external factors such as clutch maternal lineage (here called female family), area of origin and environment, on the allometric growth is discussed.

Table 3 presents the analysis of covariance (ANCOVA) of sex and age in relation to the morphometric variables taken ANCOVA here is used to compare male and female growth curves When significant (P-value < 0 100) separate growth curves are presented When not (P value ≥ 0 100) males and females are pooled together Six of eight "length" variables (TTL, SVL, BM, DCL, LCR, and PXS) and three of six "width" variables (CW, SW, and WSR) showed differences between males and females This pattern can be an indication that old males tend to be longer than females both in terms of body and head-length, which is compatible to what was described by Neill (1971) No ratio variable presented differences between males and females

Five of eight variables located on the upper jaw and cranium (DCL, CW, SW, LCR, and PXS) and one of four variables located on the lower jaw (WSR) showed differences between

males and females. Crocodilians social behavior generally involves visual displays wherein the lower jaw is kept beneath the water surface while the upper jaw and the top of the head are exposed above (for detailed studies see Garrick *et al.*, 1978; Ayarzaguena 1983; Lang 1987; and Vliet 1989).

Table 3. Analysis of covariance: sex as covariate of age on growth curves (P values)

Body-size variables	Age	Sex	Head-size variables	Age	Sex	Ratio variables	Age	Sex
TTL	0.000	0.072	DCL	0.000	0.083	RCW	0.000	0.205
SVL	0.000	0.048	CW	0.000	0.040	RLST	0.000	0.628
BM	0.000	0.055	SL	0.000	0.116	RWST	0.000	0.790
BW	0.000	0.498	SW	0.000	0.052	ROL	0.000	0.475
			OL	0.000	0.223	ROW	0.000	0.512
			OW	0.000	0.487	RWI	0.000	0.265
			IOW	0.000	0.110	RWN	0.000	0.396
			LCR	0.000	0.056	RPXS	0.000	0.301
			WN	0.000	0.533	RLSS	0.104	0.471
			PXS	0.000	0.037	RWM	0.000	0.493
			ML	0.000	0.131	RLMR	0.902	0.272
			LMS	0.000	0.250			
			WSR	0.000	0.020			
			LM	0.000	0.165			

Minitab procedure: Stat → ANOVA → General Linear Model
Response (dependent variables): morphometric variables
Model (independent variable): *Age*
Covariate: *Sex*

The predominance of upper jaw and cranium variables on the sexual dimorphism can indicate a sexual selection associated with the social behavior of crocodilians. Thus, the most exposed regions of a male body would increase in size more pronouncedly than on the female. There is a great number of analogous examples involving birds and mammals, besides the "obvious" peacock tail and lion mane (for expanded discussion and examples see Gould and Gould 1989; Anderson 1994; and Short and Balaban 1994). Sexual dimorphism and the assessment of individual gender based on cranial morphometrics is discussed later in item 4.2.4.

In the present study growth curves of 1–10 year-old captive animals are presented for all size and ratio variables (Tables 4–5; Figures 5–6). As explained above, males and females growth curves are presented together unless for the variables with a significant effect (P value ≤ 0.100) of gender on growth showed by the analysis of covariance (Table 3). With the exception

of body mass. log transformation did not improve regression equations. Thus, all other variables are presented without transformation.

Table 4. Growth curves of captive animals. Body and head-size variables.

#	Sex	Y	a	b	c	d	P value	r^2	N
1	males	TTL	13.8707	61.4776	-11.1375	0.7014	0.000	0.983	24
2	females	TTL*	16.4613	23.1788	0.8747		0.000	0.874	92
3	males	SVL	-7.6476	36.6807	5.3800	0.3394	0.000	0.987	24
4	females	SVL*	6.6947	12.4079	-0.4949		0.000	0.876	92
5	males	LogBM	-1.9904	1.3946	-0.2386	0.0135	0.000	0.972	24
6	females	LogDM	-1.0380	0.4770	0.0228		0.000	0.810	92
7	males & females	BW	63.3459	5.6616	9.6105	-0.6614	0.000	0.925	116
8	males	DCL	0.4797	54.8650	-9.2493	0.5752	0.000	0.981	24
9	females	DCL*	26.3770	23.0610	-0.8867		0.000	0.895	92
10	males	CW	-9.3663	47.3512	-8.7928	0.5811	0.000	0.986	24
11	females	CW*	15.0750	16.7860	-0.4690		0.000	0.813	92
12	males & females	SL	-4.5228	14.7511	-0.5070		0.000	0.924	116
13	males	SW	-9.7652	34.4580	5.8630	0.3778	0.000	0.984	24
14	females	SW*	9.8802	14.8827	-0.5311		0.000	0.901	92
15	males & females	OL	10.4677	4.9737	-0.2362		0.000	0.888	116
16	males & females	OW*	7.7007	2.3895	-0.0831		0.000	0.861	116
17	males & females	IOW	0.3782	2.6441	-0.0742		0.000	0.911	116
18	males	LCR	3.3711	12.6070	-2.1748	0.1347	0.000	0.991	24
19	females	LCR*	9.2046	5.3671	0.2386		0.000	0.890	92
20	males & females	WN	3.4076	3.3332	0.1094		0.000	0.921	116
21	males	PXS	-0.5009	11.7887	1.7520	0.1027	0.000	0.988	24
22	females	PXS*	0.9518	7.0603	-0.3617		0.000	0.823	92
23	males & females	ML	19.5056	33.2922	1.3055		0.000	0.912	116
24	males & females	LMS	3.2741	4.6002	-0.1602		0.000	0.917	110
25	males	WSR	10.9183	45.7650	-8.6198	0.5757	0.000	0.972	24
26	females	WSR*	14.8476	14.8149	-0.3326		0.000	0.913	92
27	males & females	LM**	10.4766	10.6637			0.000	0.693	98

$Y = a + bX + cX^2 + dX^3$ X = age in years

Minitab procedure: Stat → Regression → Fitted Line Plot (*Polynomial Regression*)

With the exception of BM, variables were not transformed because their orders of magnitude were similar so transformation did not improve results.

Cubic element (d) was included in the equation ($d \neq 0$) whenever significant (P value ≤ 0.05).

Quadratic element (c) was included in the equation ($c \neq 0$) whenever either quadratic or cubic element were significant (P value ≤ 0.05).

Males and females presented separately when ANCOVA for sex was significant (P-value < 0.100). See Table 3 for P values.

* Although cubic equation would best express variables, the quadratic regression was preferred because cubic element would result in decreasing values of "Y" at greater values of age, which does not make sense in biology.

** Growth curves for LM and RLLMR were developed only for the ages of one through five years.

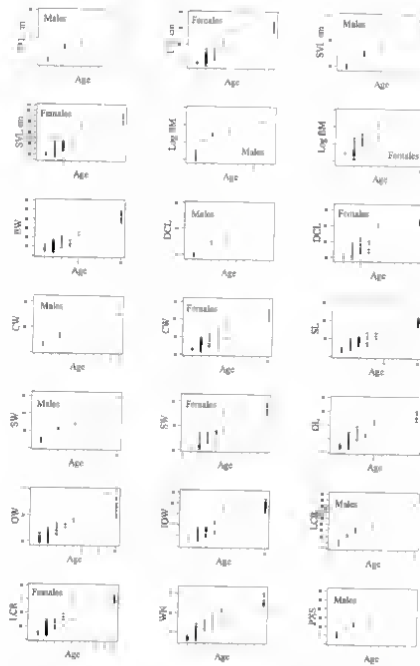


Figure 5. Plots of growth of captive animals. Body- and head-size variables. Age in years. Males and females presented together unless stated otherwise. See Table 3 for growth differences between sexes. See Table 4 for regression equations.

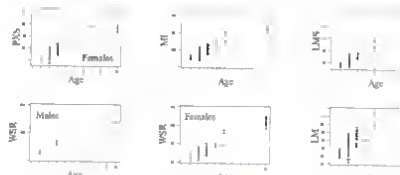


Figure 5 (cont.). Plots of growth of captive animals. Body- and head-size variables. Age in years. Males and females presented together unless stated otherwise. See Table 3 for growth differences between sexes. See also Table 4 for regression equations.

Table 5. Growth curves of captive animals. Ratio variables.

#	Sex	Y	a	b	c	d	P value	r^2	N
1	males & females	RCW	0.6389	0.0174			0.000	0.794	116
2	males & females	RLST	0.3589	0.0549	-0.0032		0.000	0.835	110
3	males & females	RWST	1.2981	-0.0650	0.0043		0.000	0.423	116
4	males & females	ROL	0.3265	-0.0223	0.0011		0.000	0.758	116
5	males & females	ROW	1.0145	-0.3357	0.0762	-0.0047	0.000	0.473	116
6	males & females	RWI	0.1424	0.0696	-0.0031		0.000	0.802	116
7	males & females	RWN	0.2859	0.0288	-0.0013		0.000	0.714	110
8	males & females	RPXS	0.2143	-0.0209	0.0081	-0.0006	0.000	0.198	110
9	males & females	RLSS	0.1409	0.0002			0.557	0.004	116
10	males & females	RWM	0.5645	-0.0175	0.0022		0.060	0.344	116
11	males & females	RLLMR	0.5733	-0.0772	0.0131		0.000	0.255	98

$Y = a + bX + cX^2 + dX^3$; X = age in years

Minitab procedure: Stat → Regression → Fitted Line Plot (Polynomial Regression)

Cubic element (d) was included in the equation ($d \neq 0$) whenever significant (P-value ≤ 0.05).

Quadratic element (c) was included in the equation ($c \neq 0$) whenever either quadratic or cubic element were significant (P-value ≤ 0.05).

Males and females presented together because ANCOVA for sex was not significant (P-value ≥ 0.100). See Table 3 for P values.

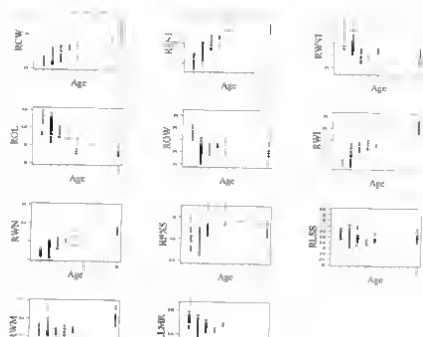


Figure 6 Plots of growth of captive animals. Ratio variables. Age in years. Males and females presented together. See Table 3 for ANCOVA of sex and age. See Table 5 for regression equations

Body and head-size variables' growth curves presented high coefficients of determination (r^2). i.e. the proportion of the variation of one variable determined by the variation of the other. Eighteen of twenty seven equations presented $r^2 > 0.900$ whereas the others presented $0.800 < r^2 < 0.900$ with only one exception: LM ($r^2 = 0.683$). This means that the models proposed are efficient to explain most of the variation presented. Males presented higher coefficient of determination than females possibly because of their smaller sample size (Table 4, Figure 5).

Ratio variables presented lower and more variable coefficients of determination, varying from virtually zero on RLSS to 0.835 on RLST (Table 5). This means that age is not a consistent source of variation for the former as it is for the later, which can be easily visualized in Figure 6.

This also means that ratio variables are generally less age-dependent than body and head size variables

Avery (1994) suggests that growth data for small and medium-sized reptiles are best fitted by logistic-by mass equations whereas data for larger reptiles are best fitted by the von Bertalanffy equation. Brisbin (1990) reports that both the Richards and the von Bertalanffy sigmoid model described the growth of captive male and female alligators equally well, but the Richards model explained significantly more variation for wild alligators. Hall and Porter (1994) suggests that both methods are less efficient than Brody's model (Brody 1945) to fit growth data for *Crocodylus novaeguineae*. Abercrombie (1992, 1996) suggests that either the von Bertalanffy or the full Richards model may often be used (carefully) for summarizing the growth of crocodilians the former being more appropriate to compare results with other published data, and the latter possibly better to specify technical error

The SVL growth curve of the present study is surprisingly similar to the one presented by Magnusson and Stanvitch (1995) for *Caiman crocodilus crocodilus* in Central Amazonia, Brazil. On the other hand SVL growth curves for BSC in coastal environment of *Ilha de Cardoso*, São Paulo State, Brazil presented a much slower growth rate possibly because of water high salinity rate (Moulton *et al*., in press)

Using both Richards and von Bertalanffy growth models, Moulton *et al* (in press) suggest an asymptotic SVL from 97 to 107 cm with the age of female first reproduction varying from 8.6 years (60 cm SVL) to the possible mean of 13 to 15 years (≈ 75 cm SVL). The present study suggest a period of 5 to 10 years for the female to reach sexual maturity (≈ 65 cm SVL), which is compatible to the possible size of females at sexual maturity in Santa Fe, Argentina (Larriera, pers. comm.) and to the actual age at first reproduction (9 to 10 years) observed in captivity in São Paulo, Brazil (Verdade in press)

Females sampled in this study showed a clear tendency of reaching asymptotic values of most body-and head-size variables and some ratio variables from 5 to 10 years of age. As explained above on item 4.1 sample error may explain the best fit of cubic rather than quadratic equations for females in some variables (see Table 4). In these cases, quadratic equations were preferred because the use of cubic equations would lead to a decrease in the animal size after a certain age which would not make biological sense in this case

4.2.2 Age Estimation

Many techniques are used to determine age in vertebrates. Some are simple and easily employed without special training, but for some species sophisticated techniques are required. According to Larson and Taber (1980), the criteria for ideal age determination should have the following characteristics: "independence from irregular nutritional and physiological variations" "clear separations into age classes or year classes without subjective judgement" "suitability for living animals of all ages" and "ease of application by semiskilled technicians". Although some standard techniques meet these criteria for some species, Larson and Taber assume that most do not. For these cases, they propose that one or more of the ideal criteria must be compromised depending on the degree of accuracy required, in order to obtain the information needed.

While plumage characteristics are generally used to establish age classes in birds (Dunnick and Pelton 1996), the standard techniques for post-embryonic age determination in mammals involve horns' annual rings (Branberg 1955), eye-lens weight (Friend 1967), cementum annuli of teeth or long bones' periosteal zone (Klevezal and Klemenberg 1967), tooth eruption, replacement and wear (Larson and Taber 1980), and growth-layer-group counts in bone (Marmontel *et al.*, 1996). Larson and Taber (1980) and Dunnick and Pelton (1996) present extensive reviews on aging techniques for birds and mammals on the traditional wildlife management approach.

Age determination of fish is essential in fisheries management decisions (Panly 1987). Although recent studies have demonstrated that scale ages for some species can result in serious underestimates (Beamish and McFarlane 1987), the following standard techniques are generally used depending on the species life span: daily growth rings (Panella 1971, 1974), annual growth annuli (Casselman 1987), length-frequency and modal progression analyses (Panly 1983), and age-growth related models (Panly 1987). Das (1994) presents a comprehensive review on the age determination of fishes.

Halliday and Verrel (1988) analyze four methods of age determination in amphibians and reptiles: recapture of known individuals, extrapolation from size-frequency data, skeletochronology, and testis ablation (for some salamanders). They question the common assumption that body size and age are strongly correlated in adult amphibians and reptiles, and conclude that only two of the methods above are reliable: skeletochronology and mark-recapture.

Skeletochronology is based on the observation that growth in amphibians and reptiles is periodic and that its temporal pattern is recorded in certain bones (Senning 1940), and in the epidermal scutes of chelonians (Cagle 1946). This technique usually consists of counting annual

layers to bony tissues (Smirina 1994). Mark recapture techniques are based on the growth record of animals of known age and the application of growth models that best fit these data (Andrews 1982)

Annual growth rings in phalanges were useful to determine age of three European frogs (Gibbons and McCarthy 1983). Skeletochronology was more efficient than logistic by-mass growth model (based upon mark-recapture data) in order to estimate life span and the relationship between size and age in long-toed salamanders (*Ambystoma macrodactylum krausei*) in southwestern Alberta, Canada (Russel *et al* 1996). Smirina (1994) presents an inclusive review on the age determination and longevity of amphibians.

Mark recapture, external annuli and bone rings are also proposed by Gibbons (1976) as the primary methods of aging reptiles, however, skeletochronology is in general considered the most precise method of age determination in reptiles (Castanet 1994). Examples concerning snakes (Castanet 1974), sea-turtles (Zug *et al*., 1986, Klinger and Musick 1995, Bjorndal and Zug 1995), lizards (Chinsamy *et al* 1995), and crocodiles (de Buffrénil 1980, Ferguson 1984, Hutton 1986, 1987) corroborate this opinion

Although skeletochronology is an excellent post mortem technique its application to living crocodilians is still in its beginning (Hutton 1987). The impossibility of its use in living animals has prevented its use for rare or endangered species such as the BSC. Therefore mark recapture experiments and the subsequent application of growth models such as von Bertalanffy and Richards are still widespread (Brisbin 1990). However, growth curves based on single body size measurements are usually considerably imprecise as age predictors for crocodilians because of their great variation on growth rates even within a single population (Hutton 1987).

Deviations from simple growth curves (so-called "outsiders") are generally not considered or regarded as of little biological meaning. On the other hand, the description of relative growth on a multivariate context, with several axes of variation, would be more effective to capture deviations from the growth curve when they are found to be correlated. This would prevent loss of biological information (Jolicoeur and Mosimann 1960). Willig *et al* (1986) and Willig and Owen (1987) propose that "because MANOVA utilizes rather than ignores correlations among characters, it is the correct statistical test for evaluating overall group differences" in systematic studies.

In the present study an alternate multivariate approach is proposed for the study of age determination in BSC. Age-classes (one-, two-, three-, four-, and five year old animals) are considered distinct groups and the hypothesis presented on Figure 3 are tested. Univariate and

multivariate discriminant analysis of body and head-size and ratio variables are compared as age predictors Finally as an exploratory exercise, the best subset multiple regressions developed for one through five year-old captive animals are used for the estimation of wild animals age

4.2.2 1 Age discriminatioo of captive animals (1—5 years old)

There is a significant difference (P-value < 0 000) between age-classes (one-, two- three -four - and five-year old animals) in terms of the whole set of head size variables log-transformed head-size variables, and ratio variables for Wilk s Lawley Hotelling, and Pillai s Tests of MANOVA This means that the variance among groups is bigger than the variance intra groups, which answers our first question (see Figure 3)

The second question tested was Can the age-class le which a specific individual belongs be predicted? In order to answer this question, linear discriminant analyses with cross-validation were run for untransformed head-size variables (Table 5) log transformed head-size variables (Table 6) and ratio variables (Table 7) The overall proportion of correct classification was similar for the three kinds of variables varying from 0 765 (76 5%) for ratio and log-transformed variables to 0 786 (78.6%) for untransformed head-size variables

There was however a significant variatioo among age-classes in terms of the proportion of correct classification for the three types of variables It varied from 0 837 to 1 000 for one-year old, from 8 836 to 8.852 to two-year-old from 8.385 to 0 538 for three year-old, from 0 000 to 0 200 to four-year old, and from 0 336 to 0 667 to five year-old animals

Untransformed head-size variables presented consistently better results than the ratio and log transformed variables The one-year old class was consistently better discriminated than the others, whereas the four-year old class presented consistently the worst results. Most of the four year old animals were misclassified as three-year old This possibly can be explained by the squared distance between groups Age classes three and four were the closest of all Thus means that during this period few ontogenetic variations occur On the other hand the one-year old class was the most "distant" one This means that there is a consistent ontogenetic variation from the first to the second year of age, which is easy to see even with a little familiarity with crocodilians This pattern was also reported by Mook (1821a)

PCA for the whole sets of untransformed head size variables (Table 8), log-transformed variables (Table 9), and ratio variables (Table 10) and their plots (Figure 7) are useful to visualize how much the different age-classes are clustered apart. For both untransformed and log

transformed head-size variables the majority of the variance is included on the first principal component (0 946 and 0.948 respectively) (see eigenvalues in Tables 8 and 9). This means that the majority of variance between age-classes is caused by overall head size change

Table 5 Linear discriminant analysis Response: age of captive animals Predictors: all head size variables Sample size: 98 animals Groups: 1 - 5 years old.

a) Summary of classification with cross-validation

Group	1	2	3	4	5
1	15	4	0	0	0
2	0	52	2	0	0
3	1	4	7	4	1
4	0	1	4	1	0
5	0	0	0	0	2
Total N	16	61	13	5	3
N Correct	15	52	7	1	2
Proportion	0 937	0.852	0 538	0 200	0 667

N = 98 N Correct = 77 Proportion Correct = 0 786

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN	PXS
1	-127 10	2 32	5 65	-5 86	-1 14	6.16	14 08	7 98	10 51	2 12	1.69
2	-132.39	2.03	-4 87	-5 90	-0 56	8 27	10 84	8 12	11 94	2 37	1.21
3	-157 74	1 70	-6 98	-4 56	-0 35	7 98	13 76	9 01	12 03	1 99	2.49
4	-164 83	0 60	-5 41	-4 94	-0 94	8 38	14 35	10 57	12 50	1.30	2.65
5	-205 14	3 75	-13 55	5 34	3.27	3 67	14 97	11 35	12.09	2.65	3 28

	ML	LMS	WSK	LM
1	0 10	1 40	-0 02	0.60
2	0 15	-1 43	-0 69	-0 13
3	0 11	-0 31	-0 33	0 30
4	0 65	2 19	-0 57	-0 35
5	-0.25	-0 96	1.24	2.24

The coefficients of untransformed variables for the first principal component are quite similar, varying in absolute terms from 0 248 to 0 273 (see PC1 in Table 8), whereas log transformed variables presented coefficients varying from 0 125 to 0.353 (see PC1 in Table 9). This means that log-transformation stressed the role of some specific morphometric variables during ontogenetic variation during aging process. Snout length (SL) and inter-orbital width (IOW) were the variables that contributed with more variation according to the PCA of log transformed variables. This may mean that during the first five years of age the snout gets longer

and the distance between eys gets bigger in an allometric relation with the whole head Allometric relations will be discussed later in section 4.2.3

Table 6 Linear discriminant analysis Response: age of captive animals. Predictors: all log-transformed head-size variables Sample size: 98 animals Groups: 1=5 years old

a) Summary of classification with cross-validation

Group	1	2	3	4	5
1	16	2	0	0	0
2	0	51	0	0	0
3	0	6	6	5	1
4	0	2	6	6	0
5	0	0	1	0	2
Total N	16	61	13	5	3
N Correct	16	51	6	0	2
Proportion	1.000	0.836	0.462	0.000	0.667

N = 98 N Correct = 75 Proportion Correct = 0.765

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
1	-2332.9	5733.6	285.9	2793.2	-909.5	534.9	563.0	30.3	286.0	856.3
2	-2323.3	5615.7	414.8	2694.0	-830.9	394.3	447.3	35.3	309.5	-881.0
3	-2315.0	5614.1	246.6	2645.5	-841.6	392.6	522.4	53.1	322.5	-874.3
4	-2345.4	5512.6	334.7	2659.7	-857.4	381.4	532.1	54.1	367.1	-868.6
5	-2416.0	5898.4	317.6	2758.4	-690.0	533.9	539.0	54.9	371.2	-929.3

	PXS	ML	LMS	WSR	LM
1	28.4	994.0	-637.5	-829.2	27.0
2	28.0	988.3	-641.9	-916.8	138.6
3	-8.3	967.6	-619.4	892.2	113.5
4	6.8	1060.7	-671.6	898.7	-164.2
5	6.2	917.2	-615.3	804.9	-45.6

The second principal components for both untransformed and log-transformed head-size variables contributed with 0.016 (1.6%) and 0.024 (2.4%) of the total variance respectively (see PC2 in Tables 8 and 9) The major source of variation for the second principal component of untransformed variables was the orbital width (OW), which contrasts with the other two eye measurements (OL and IOW) in magnitude and sign This pattern captures a rearrangment of the eye-orbits on the head during the first five years of age They become relatively longer (OL with positive sign) and narrower (OW with negative sign) while the distance between the eyes increases (IOW with positive sign).

Table 7 Linear discriminant analysis. Response: age of captive animals Predictors: all ratio variables Sample size: 98 animals Groups: 1 5 years old

a) Summary of classification with cross-validation

Group	1	2	3	4	5
1	16	2	0	0	0
2	0	52	2	0	0
3	0	5	5	4	2
4	0	2	5	1	0
5	0	0	1	0	1
Total N	18	61	13	5	3
N Correct	16	52	5	1	1
Proportion	1.000	0.852	0.385	0.200	0.333

N = 98 N Correct = 75 Proportion Correct = 0.765

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS	RLSS
1	-2664.8	-606.6	5273.9	1133.5	4135.2	879.2	453.6	-1505.8	271.0	947.2
2	-2654.0	-584.9	5386.7	1130.5	4157.5	865.5	465.5	-1573.6	287.4	1028.5
3	-2717.9	-648.9	5500.0	1142.4	4146.3	871.5	464.2	-1541.1	317.7	1072.5
4	-2726.0	-599.8	5467.7	1135.3	4221.0	834.3	495.4	-1548.9	329.1	917.4
5	-2710.7	-803.3	5553.6	1203.3	3957.9	816.6	484.1	-1495.8	340.8	1008.0

	RWM	RLLMR
1	260.8	354.6
2	321.0	248.9
3	311.2	276.0
4	311.9	235.0
5	315.4	346.9

The inter-orbital width (IOW) is the variable that contributes most for the variance contained in the second principal component of the log-transformed PCA. There is a clear contrast between it and the mandibular variables (ML, LMS, WSR, and LM) in both magnitude and sign. This pattern possibly captures the widening of the eye region (but not exactly the eye orbits) of the head in relation to the mandible.

The PCA of ratio variables showed, as could be expected, a completely different pattern. The first principal component contributed with less than half of the total variation, while the second principal component accounted for almost one fourth of the total variation (see eigenvalues in Table 10). The intrinsic shape component of ratio variables made the PCA difficult to interpret. There seems to be a contrast between the relative width and the relative length of snout (compare signs and magnitudes of RLST and RWST on PC1 in Table 10). There also seems to be a contrast between the relative orbital width (ROW) and the relative inter-orbital width (RWI) (compare their signs and magnitudes on PC1 in Table 10). These two contrasts

above are the major sources of variation for the first principal components There may be a "size" component on the contrasts described above in the sense that these ratios are not completely size-independent (see Figure 10 and the discussions on allometric relations in section 4.2.3), but this is rather complex and subjective

The contrast involving RWST and ROW is the major source of variation on the second principal component (see PC2 on Table 10) This pattern may also have captured a rearrangement of the eyes region during ontogenetic change on the first five years of age in the sense that the snout becomes broader (RWST with positive sign) and the eyes orbits become narrower (ROW with negative sign)

On Figure 7a, c and e it is possible to see the distribution of animals against the values for the two principal components of the whole set of untransformed, log-transformed and ratio variables respectively One year old animals are clustered apart in all of them which is compatible to the pattern showed by the linear discriminant analysis. Assuming PC1 as the "size" component and PC2 as the main "shape" component, and considering the distribution of individuals on the plots it is possible to infer that there is a consistent ontogenetic variation both in size and shape during the first year of age Two-year old animals are consistently put apart with both untransformed and log-transformed, but not with ratio variables On the other hand, animals from three to five years of age present a less evident separation.

Table 8 Principal components analysis Eingenalysis of the correlation matrix of all head-size variables. Sample size 98 animals Only six first principal components are presented

Eigenvalue	13.790	0.230	0.135	0.105	0.059	0.046
Proportion	0.949	0.016	0.010	0.008	0.004	0.003
Cumulative	0.949	0.966	0.975	0.983	0.987	0.990
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0.272	0.126	0.110	0.027	-0.076	-0.047
CW	-0.273	0.124	0.963	-0.081	0.036	-0.021
SL	-0.272	0.090	-0.021	-0.059	-0.123	-0.152
SW	-0.272	0.126	0.084	0.005	0.115	-0.017
OL	-0.263	0.329	0.519	-0.034	-0.387	0.201
OW	-0.248	-0.811	0.248	-0.431	-0.122	0.060
IOW	-0.259	0.216	-0.568	-0.530	-0.117	0.090
LCR	-0.279	0.141	0.133	-0.084	0.148	-0.021
WN	-0.270	-0.071	-0.173	-0.060	0.208	0.012
PXS	-0.262	-0.233	-0.342	0.562	-0.588	-0.197
ML	-0.270	0.027	0.052	0.046	0.421	-0.457
LMS	-0.267	-0.074	-0.102	0.311	0.264	0.691
WSR	-0.272	0.112	0.127	0.009	0.157	-0.095
LM	-0.269	-0.175	-0.050	0.293	0.328	-0.148

Table 9 Principal components analysis Eingenalysis of the covariance matrix of all log-transformed head size variables Sample size 98 animals Only six first principal components are presented

Eigenvalue	0 19954	0 00435	0 00238	0 00100	0 00074	0 00058
Proportion	0 948	0 021	0 011	0 005	0 004	0 003
Cumulative	0.948	0 969	0 981	0 985	0 989	0 992
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0.247	-0.045	0 181	-0 038	-0.162	-0.014
CW	-0.279	-0 018	0 212	-0 051	-0 117	0 065
SL	-0 520	0.031	0 368	-0 094	-0.255	-0 040
SW	-0 295	-0 018	0 265	-0 066	-0 058	-0 044
OL	-0.189	-0 045	0 310	-0 168	-0 097	-0 879
OW	-0.125	-0.170	-0 241	0 740	-0.478	0.022
IOW	-0.355	0.874	-0 203	0 096	0.159	-0.058
LCR	-0 165	0 003	0 155	0.006	-0 196	0.051
WN	-0 256	-0.030	-0 106	0 200	-0 078	0 220
PXS	-0 381	-0.230	-0 676	-0 515	-0 267	-0 238
ML	-0.292	-0 154	0.091	0 105	0 515	-0 214
LMS	-0.276	-0 152	-0 150	-0.116	0 240	0 357
WSR	-0.276	-0 086	0.259	-0.001	0 032	-0.115
LM	-0.277	-0 369	-0 176	0 261	0 602	-0.292

Table 10 Principal components analysis Eingenalysis of the covariance matrix of all ratio variables Sample size 98 animals Only six first principal components are presented

Eigenvalue	0 010510	0 005186	0.002719	0 001000	0 000903	0 000520
Proportion	0 482	0 242	0 127	0 047	0 042	0 024
Cumulative	0 482	0 724	0 852	0 898	0 940	0 965
Variable	PC1	PC2	PC3	PC4	PC5	PC6
RCW	0 185	0 055	-0 328	-0.020	0.192	-0.582
RLST	0 342	-0 125	-0.078	0.012	0 167	-0.345
RWST	-0 480	0 508	-0 653	-0 069	0 146	0 054
ROL	-0 125	0 136	0 151	0 901	0 036	-0 077
ROW	-0.581	-0.757	-0 174	-0 129	-0 130	-0 151
RWT	0 457	-0 249	-0.505	0.072	-0.323	0 441
RWN	0 181	-0 165	-0 174	-0.024	0.257	-0.276
RPXS	0 036	-0 144	-0 090	0 109	0 434	0.007
RLSS	-0 022	-0 021	-0 004	0 168	-0 842	0 027
RWM	-0.074	0 157	-0 048	0 571	-0 600	-0.431
RLLMR	-0 125	-0 154	0 096	0 778	0 419	0 235

Table 11 presents the best subsets of variables for age determination Untransformed head-size variables present the best results in terms of the regression equations coefficients of determination Logtransformation of data resulted in the choice of two different variables (IOW and LCR instead of SW and SL) The best subset of ratio variables showed a preponderance of relative width indices (RCW RWST and RWI), whereas length and width variables contributed equally to the best subsets of untransformed and log transformed variables

Table 11 Age regression equations based on best subsets of morphometric variables

Type of variable	Regression equations	r^2	P-value (model)
Head-size	Age = 0.517 − 0.128 CW + 0.069 SL + 0.112 SW + 0.0827 PXS	0.728	0.000
Log head-size	Age = −3.05 + 5.99 CW + 2.27 IOW + 7.90 LCR + 3.04 PXS	0.680	0.000
Ratios	Age = −7.53 + 10.5 RCW + 23.2 RLST + 4.30 RWST + 3.89 RWI	0.661	0.000

Type of variable	Best subset	P-value
Head-size	CW	0.001
	SL	0.023
	SW	0.003
	PXS	0.006
Log-transformed head-size variables	CW	0.020
	IOW	0.007
	LCR	0.014
	PXS	0.006
Ratios	RCW	0.005
	RLST	0.000
	RWST	0.007
	RWI	0.007

Minitab procedure: Stat → Regression → Best Subsets
Sample sizes: 101 captive animals

All variables chosen are located on the cranium and none on the mandible. Crocodilians have an amphibulous mode of existence, living in both aquatic and terrestrial habitats and exhibiting many behaviors at the water surface or underwater (Lang 1987). Most of the crocodilian social displays observed and described by humans involve the position of the mandible beneath the water surface, whereas the top of the head (cranium and upper jaw) is kept above it (see Garrick et al., 1978; Ayarzaguena 1983; and Vliet 1989). Although some morphological constraints may be related, this pattern stresses the possible relationship between social behavior and ontogenetic changes. The regression equations presented should of course not be extrapolated beyond the limits of the ages studied.

There is a significant difference between age-classes (one-, two-, three-, four-, and five year old animals) in terms of the best subset of head size variables, log-transformed head size variables, and ratio variables (P value < 0.000 for Wilk's, Lawley Hotelling, and Pillai's Tests of MANOVA). This means that, even reducing the number of variables, the variance among groups is still bigger than the variance intra groups, which answers the first step of the third question of the present study (see Figure 3).

Linear discriminant analysis with cross-validation are presented for the best subset of untransformed variables (Table 12), log-transformed variables (Table 13), and ratio variables (Table 14). The overall proportion of correct classification is significantly lower than for the

whole set of variables varying from 0 634 for ratio variables to 0 683 for log transformed variables, with an intermediate value for untransformed variables

Table 12 Linear discriminant analysis Response: age of captive animals Predictors: best subset of head-size variables. Sample size 101 animals Groups: 1=5 years old

a) Summary of classification with cross validation

Group	1	2	3	4	5
1	15	12	0	0	0
2	1	29	0	1	0
3	0	4	7	3	1
4	0	7	6	1	0
5	0	0	0	0	4
Total N	16	52	13	5	5
N Correct	15	39	7	1	4
Proportion	0 937	0 528	0 538	0.200	0 800

N = 101 N Correct = 66 Proportion Correct 0 653

b) Linear discriminant function for group

	Constant	CW	SL	SW	FXS
1	8 694	1 410	-1 544	-0 248	1 025
2	15 020	1 121	-1 439	0 299	0 857
3	-23 746	0 036	-0 801	0 888	1 907
4	-26.702	0.846	-1 088	0 342	1 520
5	-62 835	3 418	0 392	4 164	3.033

Table 13 Linear discriminant analysis Response: age of captive animals Predictors: best subset of log-transformed head size variables Sample size 101 animals Groups: 1 5 years old

a) Summary of classification with cross-validation

Group	1	2	3	4	5
1	15	0	0	0	0
2	1	45	2	0	0
3	0	4	4	2	1
4	0	5	7	2	1
5	0	0	0	1	3
Total N	16	62	12	5	5
N Correct	15	45	4	2	3
Proportion	0 937	0 726	0 308	0 400	0 600

N = 101 N Correct = 69 Proportion Correct = 0 683

b) Linear discriminant function for group

	Constant	CW	IOW	LCR	FXS
1	389 76	279 78	-275 19	581 04	174 45
2	-429 28	302 61	-250 99	592 94	-193 90
3	-436 05	249 92	-246.45	625 96	-157.61
4	-447 47	255 62	242 66	633 54	-166 64
5	-494 86	220 20	-242.65	696 27	-156 51

Table 14 Linear discriminant analysis Response age of captive animals Predictors best subset of ratio variables Sample size 101 animals Groups 1 5 years old

a) Summary of classification with cross-validation

Group	1	2	3	4	5
1	14	10	0	0	0
2	2	39	3	2	0
3	0	4	5	1	0
4	0	0	4	2	1
5	0	0	1	0	4
Total N	16	62	13	5	5
N Correct	14	39	5	2	4
Proportion	0 875	0 629	0 385	0 400	0 800

N = 101 N Correct = 64 Proportion Correct = 0 634

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	RWI
1	564 9	-910 5	2629 1	947 5	-249 3
2	576.3	971 9	2744 4	963 6	-250 7
3	-617 6	996 9	2843 6	968 4	249 8
4	-572 1	-1011 7	2808 6	964 6	236 0
5	762 0	1075 0	3005 9	1033 0	188 0

Similarly to the pattern shown by the discriminant analysis of the whole set of variables there was a significant variation among age-classes in terms of the proportions of correct classification for the three types of variables It varied from 0 875 to 0 937 for one year old from 0 629 to 0 726 for two-year old, from 0 308 to 0 538 for three-year old, from 0 200 to 0 400 for four year old and from 0 600 to 0 800 for five-year old animals

Log transformed variables presented slightly better results than their untransformed counterparts Five-year old animals were the most distant group from all the others Two-, three- and four-year old groups were considerably close to each other Two-year old animals were also close to the one-year group. This means that the reduction in the number of variables resulted on a slightly lower efficiency in discrimination animals from intermediate ages, although the same efficiency is reached to put the extreme age-classes analysed apart

PCA for the best subsets of untransformed head size variables, log-transformed head-size variables and ratio variables (Table 15) and their plots (Figure 7b, d, f respectively) are useful to visualize how much the different age-classes are clustered apart after the reduction on the number of variables PC1 is responsible for most of the variation for the three kinds of variables, varying from 0 731 for ratio to 0 974 for untransformed variables which in its turn is quite similar to the result for the log-transformed variables. This means that the overall size variation,

as the major ontogenetic change for the age-classes analyzed could be captured by the best subset of variables as well

Similar to the pattern showed by the PCA for the whole set of untransformed and log transformed variables the PC1 coefficients were more variable for the later than for the former (see PC1 in Table 15a and b) This means that log-transformation is still more sensitive to the role of specific variables on the overall size change of the head even with a reduced number of variables Inter orbital width (IOW) is still the major source of variation in this case

Table 15 Age discrimination of captive animals Principal components analyses of best subsets of variables Sample size: 101 animals

a) Eingenalysis of the correlation matrix of best subset of head size variables

Eigenvalue	3 8959	0 0870	0 0128	0 0044
Proportion	0 974	0 022	0 003	0 001
Cumulative	0 974	0 996	0 999	1 000
Variable	PC1	PC2	PC3	PC4
CW	-0.504	0.380	0 170	0.792
SL	-0 504	0 164	-0.823	-0.206
SW	0 502	0 375	0.526	-0 574
PXS	-0 490	0.832	0 132	0.214

b) Eingenalysis of the covariance matrix of best subset of log-transformed head-size variables

Eigenvalue	0 076461	0 003024	0 001276	0 000165
Proportion	0 944	0 037	0 016	0 002
Cumulative	0 944	0 982	0 998	1 000
Variable	PC1	PC2	PC3	PC4
CW	-0 482	-0 189	0 598	0 611
IOW	-0 639	0 715	-0.282	-0.007
LCR	-0.345	-0 122	0 401	-0 790
PXS	-0 490	-0 662	-0.566	-0.036

c) Eingenalysis of the covariance matrix of best subset of ratio variables.

Eigenvalue	0.0094646	0 0027896	0 0005886	0 0001100
Proportion	0 731	0.215	0 045	0 008
Cumulative	0 731	0 946	0.992	1 000
Variable	PC1	PC2	PC3	PC4
RCW	0 102	-0 338	-0 687	0 614
RLST	0.403	-0 070	-0 519	-0 750
RWST	-0 625	-0 742	-0 025	-0.241
RWI	0 641	-0 573	0 508	0 053

PC2 accounted for 0 022 and 0 037 of the total variation for untransformed and log transformed variables respectively A contrast between PXS and the other variables is clear on

PC2 of the former (see PC2 in Table 15a) This pattern captures a rearrangement of the anterior part of the snout in relation to the rest of the head in the sense that this region becomes relatively shorter (PXS with negative sign) PC2 of best subset of log transformed variables in its turn shows a contrast between IOW and PXS This may be related to the widening of the inter-orbital distance and the anterior region of the snout which is comparible with the results of the PCA for the best subset of untransformed variables.

Once again PCA of ratio variables showed a complex pattern There is a contrast on PC1 between the relative width of snout (RWST) and the relative inter-orbital width (RWI) There may be a "size" component in this contrast since it is related to two relative width indices, but its biological meaning is uncertain PC2 (see Table 15c) accounts for 0.215 of the total variation contained on the PCA for ratio variables. It presents all coefficients with the same sign RWST and RWI are the major sources of variation again However at this time they may represent a "residual" shape change relative to the same contrast described above but this is also rather complex and subjective

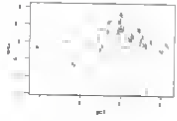
On Figura 7b, d and f it is possible to see the distribution of animals against values for the two principal components of the best subsets of untransformed, log-transformed and ratio variables, respectively It is also possible to compare these results with the ones presented by similar plots of the whole sets of variables Finally, it possible to infer the convenience of transforming data and working with ratios instead of raw measurements

Log transformation of head-size variables did not significantly improve the results of any of analyses above Ratio variables showed complex and subjective pattern on the principal components analysis of both the whole set and the best subset of variables In addition they were always inferior to the metric variables. One-year old animals were efficiently discriminated with both the whole set and the best subset of variables Five and four-year old animals, however were classified more efficiently with the best subset of variables than with the whole subset. Three-year old group remained the same after the reduction of the number of variables, whereas two-year old animals presented worst results with best subset

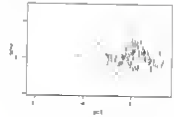
Table 16 presents a comparison between univariate and multivariate discriminant analysis of age in captive animals Proportions of correct estimates are presented for different multivariate combinations of variables and single variables for four distinct age classifications

There is a consistent improvement of the efficiency of both univariate and multivariate discriminant analysis when age-classes are pooled together Pooling three- and four-year old together improved the models significantly better than pooling two- and three year groups

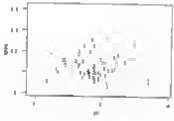
together However best results were obviously obtained pooling two- three and four year old animals together Considering the precision needed this procedure can be justified



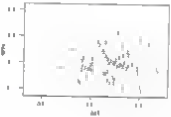
a) All head-size variables



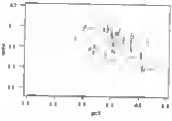
b) Best subset of head-size variables



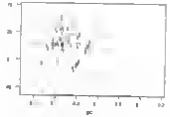
c) All log transformed head size variables variables



d) Best subset of log-transformed head-size



e) All ratio variables



f) Best subset of ratio variables

Figure 7 Age discriminatee of captive animals based on head morphometry Plots of captive animals ages (years) against values for the two principal components

Table 16 Comparative efficiency of multivariate versus univariate discriminant analysis of age in captive animals Proportions of correct estimate of age based on discriminant analysis with cross-validation

Age groups (years) / Variables	1 2–3 4 5	1–(2–3) 4–5	1 2 (3–4) 5	1 (2 3 4) 5
(DCL LM) + SVL	0 796	0 827	0 878	0 918
DCL LM	0 786	0 827	0.898	0 918
RCW RLLMR	0 765	0 816	0 878	0 939
Log DCL – Log LM	0 765	0 806	0 898	0 949
SVL	0 574	0 683	0.653	0 802
BM	0 604	0 594	0 673	0 673
HW	0 495	0 564	0.574	0 683
DCL	0 614	0 693	0.673	0 832
CW	0 624	0 693	0.673	0 812
SL	0 644	0 663	0 723	0 802
SW	0 584	0 693	0 673	0 842
OL	0 545	0 663	0.644	0 812
OW	0 455	0 455	0 495	0 535
IOW	0 584	0.604	0 653	0 792
LCR	0.614	0 663	0 693	0 802
WN	0.574	0 634	0.663	0 752
PXS	0 594	0 545	0 673	0 703
ML	0.594	0 693	0 693	0 792
LMS	0 594	0 604	0 693	0 772
WSR	0 604	0 693	0.683	0 812
LM	0 582	0 622	0 653	0 755
RCW	0 337	0 495	0 366	0 515
RLST	0 594	0 663	0 644	0 743
RWST	0.426	0 386	0 465	0 426
ROL	0 485	0.426	0 574	0 594
ROW	0.545	0 644	0 594	0 703
RWI	0 525	0 545	0 574	0.644
RWN	0.406	0 455	0 455	0 515
RPXS	0 446	0 436	0 505	0 505
RLSS	0.220	0 337	0.455	0.574
RWM	0 416	0 465	0 465	0 495
RLLMR	0.327	0.439	0 541	0 755

Minitab procedure Stat → Multivariate → Discriminant → Cross validation
DCL LM all 14 head-size variables
RCW RLLMR all 14 ratio variables
Log DCL – Log LM all 14 log transformed head size variables
1 2 3 4 5 ages 1 through 5 years analysed separately
1 (2–3) 4 5 ages 2 and 3 years pooled together
1 2–(3–4) 5 ages 3 and 4 years pooled together
1 (2 3 4) 5 ages 2 through 4 years pooled together

Univariate analyses were consistently less efficient than multivariate analyses on the estimate of age. Univariate discriminant analysis presented a proportion of correct estimate of age varying from 0 220 (RLSS) to 0 644 (SL) for all age groups analyzed separate, and from

0 495 (RWM) to 0 842 (SW) for two- three-, and four-year old groups together Snout vent length (SVL) alone varied from 0 574 to 0 802 according to the age-classification used Body mass varied from 0 604 to 0 673 in the same circumstance Multivariate discriminant analysis presented a proportion of correct estimate of age varying from 0 765 (all log-transformed and ratio variables) to 0 796 (all head-size variables with SVL) and from 0 918 (all head-size variables with or without SVL) to 0 945 (all log-transformed head-size variables) for two- three- and four year old groups together

The inclusion of SVL does not significantly improve the model On the contrary its efficiency slightly decreases when three- and four-year old animals are pooled together This explains why growth curves of single variables are not efficient to predict age. Snout vent length and body mass, the most utilized body-size measurements for crocodilians, are less efficient to predict age than for instance dorsal cranial length (DCL) snout length (SL) or cranial width (CW), which is surprising, considering that few crocodilian specialists would propose age estimation models with these variables but many did with SVL and BM

These results show that cranial morphometry *may* capture more efficiently ontogenetic changes even when there is no consistent variation in body size. In other words, cranial morphometry can be more related to *development* than to *growth*, in the sense that development refers to the direct coordination (or redirection) of diverse processes while growth refers to biological synthesis (Brody 1945)

The practical application of such concepts is the increase in the capacity to discriminate *small* from *young* individuals which means in a last instance to separate size-dependent from age-dependent morphological processes External factors that influence growth rate, such as nutrition environment and others would apparently be less related to cranial morphometrics than to body size. If true, morphometric analysis of age determination of captive animals could be more efficient to estimate age of wild animals than single measurements related to body size This hypothesis is tested in the next section as an exploratory exercise, since no wild animals with known age were available in São Paulo, Brazil at the time of the present study

4.2.2.2 Age estimation of wild animals

The age of wild animals were estimated through the best subset regressions of untransformed and log-transformed head-size variables, and ratio variables presented in Table

11 Rounding procedure for wild animals is the same as used for the captive animals 0 > age > 1 year = 1, 1 > age > 2 = 2 2 > age > 3 = 3 3 > age > 4 = 4 and 4 > age > 5 = 5

Linear discriminant analyses with cross-validation were run for the untransformed head size variables (Table 17) log transformed head-size variables (Table 18) and ratio variables (Table 19) The estimated rounded age of wild animals was the response (dependent variable) and the best subset of variables selected for captive animals were the predictors (independent variables)

The two year old group presented a maximum (1 000) proportion of correct estimate with all kinds of variables The four-year old group also presented a maximum proportion of correct estimate with the log transformed variables. The three-year old animals were the only ones to present some misclassifications both with log-transformed and ratio variables

Table 17 Linear discriminant analysis Response estimated age of wild animals Predictors best subset of head size variables. Sample size 29 animals Groups 2 3 years old.

a) Summary of classification with cross-validation

Group	2	3
2	12	0
3	0	17
Total N	12	17
N Correct	12	17
Proportion	1 000	1 000

N = 29 N Correct = 29 Proportion Correct = 1 000

b) Linear discriminant function for group

	Constant	CW	SL	SW	PXS
2	−21 850	1 027	-0 131	3 011	1 870
3	−51 625	-3 252	0 884	4 701	2 653

The overall proportion of correct classification, even with cross-validation procedure, varied from 0 759 for the log-transformed variables to 1 000 (virtually 100%) for the untransformed variables, with ratio variables presenting an intermediate value of 0 966, which is surprisingly high Age-classes of two and three years were found with untransformed and ratio variables whereas age-classes of two, three and four were found by the best subset regression of log-transformed head size variables

The differences between untransformed and log-transformed head-size variables are possibly due to the different subset of variables employed. Most of the individuals (19 of 29) reserved the same age classification, in spite of the kind of variable used Untransformed head

size variables were possibly the best criteria utilized because its best subset equation presented the highest coefficient of determination

Table 18 Linear discriminant analysis Response estimated age of wild animals Predictors best subset of log transformed head-size variables Sample size 29 animals Groups 2 3 years old

a) Summary of classification with cross-validation

Group	2	3	4
2	6	4	0
3	0	12	0
4	0	3	4
Total N	6	19	4
N Correct	6	12	4
Proportion	1 000	0 632	1 000

N = 29 N Correct = 22 Proportion Correct = 0 759

b) Linear discriminant function for group

	Constant	CW	IOW	LCR	PXS
2	-1856 7	1554.2	829 6	990 0	-969 0
3	1079 7	1471 8	-780.3	1055 7	933 3
4	1150.6	1496 4	-749 6	1076 4	-954.3

Table 19 Linear discriminant analysis Response estimated age of wild animals Predictors best subset of ratio variables Sample size: 29 animals Groups 2 3 years old

a) Summary of classification with cross-validation

Group	2	3
2	9	1
3	0	19
Total N	9	20
N Correct	9	19
Proportion	1 000	0 950

N = 29 N Correct = 28 Proportion Correct = 0.966

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	RWI
2	-1420 6	-764 9	4050 6	1443 3	268.5
3	1528.8	770.2	4301 0	1439.9	219.6

PCA of untransformed and log transformed head size, and ratio variables (Table 20) and their plots (Figure 8) are useful to see how much these estimated age groups are clustered apart PC1 accounts for much of the variation both for untransformed and log-transformed variables (see PC1 in Table 20a and b), varying from 0 950 on the later to 0 978 on the former This means

that size change is the major source of variation between different age classes as well as it happens for captive animals PC1 coefficients are similar in magnitude and sign for untransformed variables (see PC1 in Table 20a) varying in absolute terms from 0 496 (PXS) to 0 503 (SW) PC1 coefficients for log-transformed variables (see PC1 in Table 20b) are however more variable in magnitude, varying in absolute terms from 0 356 (LCR) to 0 575 (IOW)

PC2 responds for 0 013 for untransformed variables and for 0 033 for log transformed variables (see PC2 in Table 20a and b) PC2 of untransformed variables shows a clear contrast, both in terms of magnitude and sign between PXS and the combination of CW and SW The biological meaning of this may be a possible rearrangement of the anterior part of the snout in relation to the width of the cranium and the snout, in the sense that the later becomes relatively broader (CW and SW with positive sign) in relation to the former (PXS with negative sign)

Table 20 Age estimation of wild animals Principal components analysis of best subsets of variables Sample size 29 wild animals

a) Eigenanalysis of the correlation matrix of best subset of head-size variables

Eigenvalue	3 9132	0 0507	0.0277	0 0084
Proportion	0 978	0 013	0 007	0 002
Cumulative	0 978	0 991	0 998	1 000
Variable	PC1	PC2	PC3	PC4
CW	-0 501	0 392	0 530	0 561
SL	-0 500	0 123	-0 822	0 243
SW	-0 503	0 327	0 121	0 791
PXS	-0 496	-0 851	0 171	-0 010

b) Eigenanalysis of the covariance matrix of best subset of log-transformed head-size variables

Eigenvalue	0 032936	0 001146	0 000378	0.000209
Proportion	0 950	0 033	0 011	0 006
Cumulative	0 950	0 983	0 994	1 000
Variable	PC1	PC2	PC3	PC4
CW	-0.513	-0 160	-0.252	-0 805
IOW	-0 575	0 745	0 317	0 119
LCR	-0 356	-0 010	-0 802	0 480
PXS	-0.529	-0 648	0 439	0 328

c) Eigenanalysis of the covariance matrix of best subset of ratio variables

Eigenvalue	0 003985	0 002434	0 000465	0 000107
	6	0	1	2
Proportion	0 570	0 348	0 067	0 015
Cumulative	0 570	0 918	0 985	1 000
Variable	PC1	PC2	PC3	PC4
RCW	0 020	-0 444	-0 707	0.550
RLST	0 386	-0 256	-0.446	-0 768
RWST	-0 913	-0 218	-0 096	-0 332
RWI	0 131	-0 871	0 541	0 029

PC2 of log-transformed variables show in its turn a clear contrast between PXS and IOW to the sense that the inter-orbital width increases relative to the anterior part of the snout (IOW with positive sign and PXS with negative sign). This is compatible to the pattern described above and reinforces the idea that ontogenetic changes occurring during the second and possibly third year of age lead to a widening of the median portion of the cranium in relation to the anterior part of the snout. This seems to be different from the patterns showed during the first year of age (for instance described by Monk 1921a) but no one-year old animal was captured, according to the criteria of age determination used in this study.

Ratio variables once again presented coefficients of different signs on PC1 and of the same sign on PC2. The biological interpretation of this pattern is once again rather complex and subjective. PC1 accounts for 0.570 of the total variation, whereas PC2 is responsible for 0.348. RWST was the major source of variation on PC1, whereas RWI was the major source of variation on PC2. RWI is consistently more influenced by body-size than RWST (Table 23, Figure 10).

Figure 8 shows the plots of wild animals' estimated age against values for the two principal components of the best subsets of untransformed head-size variables (Figure 8a), log transformed head-size variables (Figure 8b), and ratio variables (Figure 8c). In all of them a clear separation between age-classes is visible.

On Figure 8a and b it is possible to see that the age-classes can be almost completely separated by PC1. This means that overall size change must be the main source of variation between the age-classes found. This seems to be compatible with the more pronounced seasonality of food source and temperature that wild animals experience. On Figure 8c, on the other hand, age-classes can only be separated by a combination of values of PC1 and PC2. Is it interesting to compare the results shown with similar analysis for captive animals (Figure 7) and also with analyses of sexual dimorphism (Figure 13) and area of origin of wild animals (Figure 21).

4.2.3 Allometric Relations of Captive and Wild Animals

Allometric relations can be useful in the estimate of body size from isolated measures of parts of the body. Population monitoring of crocodilians usually involve night counts when usually only the heads of animals are visible. Thus, the relationship between length of head and total length is usually employed to establish size-class distribution for the target populations. As

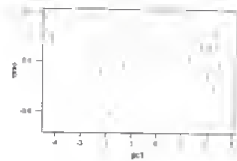
an example, Chabreck (1966) suggested that the distance between the eye and the tip of the snout in inches is similar to the total length of *Alligator mississippiensis* in feet. Choquenot and Webb (1987) propose a photographic method to estimate total length of *Crocodylus porosus* from head dimensions. In order to improve these techniques, Magnusson (1983) suggests that a sample of animals should be captured and measured. Thus relationships between estimates and actual animals' dimensions could be established and observers' bias could be corrected. The interesting point of this method is that it permits a quantification of the actual observers' bias.

Although allometric equations may lead to convenient and useful generalizations, there are important limits concerning their use. Schmidt Nielsen (1984) establishes the following points concerning them:

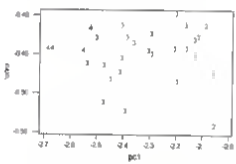
"1. Allometric equations are descriptive: they are not like biological laws."
"2. Allometric equations are useful for showing how a variable quantity is related to body size, all other things being equal (which mostly certainly they are not)."
"3. Allometric equations are valuable tools because they may reveal principles and connections that otherwise remain obscure."
"4. Allometric equations are useful as a basis for comparisons and can reveal deviations from a general pattern. Such deviations may be due to noise, or may reveal a significant secondary agent."
"5. Allometric equations are useful for estimating an expected magnitude for some variable, an organ or a function, for a given body size."
"6. Allometric equations cannot be used for extrapolations beyond the range of the data on which they are based."

In the present study, allometric relations of captive and wild BSC are presented. Table 21 shows the analysis of covariance (ANCOVA) of sex and age of captive animals in relation to the allometric equations between morphometric variables and snout-vent length (SVL). In this section ANCOVA is used to compare males and females allometric equations. It is also useful to separate age from body size effect on the morphometric variables analyzed. In later sections it is used to compare clutch and matrilineal effect on allometric relations of hatchlings and environment effect on the allometric relations of wild and captive animals of similar body size.

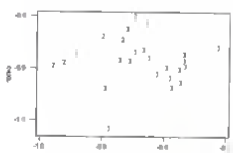
All body- and head-size variables and all but three ratio variables (RW1, RWN and RPXS) are significantly affected by body size (P value > 0.100), or in other words, they can be considered size-dependent. One body-size (BW), six head size (CW, SL, OL, OW, PXS and WSR) and one ratio variable (ROL) are significantly affected by age (P value > 0.100) i.e. they can be considered age-dependent. At last one body-size (BW), two head size (OL and OW), and five ratio variables (RCW, RLST, ROL, ROW and RWN) are significantly affected by gender (P-value > 0.100) (see Table 21).



a) Best subset of head-size variables



b) Best subset of log-transformed variables



c) Best subset of ratio variables

Figure 8 Plots of wild animals estimated age (years) against values for the two principal components

Webb and Messel (1978) report a perceptible sexual dimorphism in *Crocodylus porosus* involving interorbital width, which is not perceived in the present study. Hall and Porter (1994) found sexual dimorphism for 21 of 34 skull attributes, including DCL, ML, PXS, CW, OW, IOW, WCR, WN and WSR. However, their results are possibly optimistic because they could not include age as a covariate of body size in their study of allometric growth of *Crocodylus novaeguineae*. Some variation actually caused by age (independent of size) may be erroneously accounted as a difference between sexes, or sexual dimorphism. A multivariate approach for the study of sexual dimorphism is presented in Section 4.2.4.

Table 21. Analysis of covariance. Age and sex as covariates of SVL (F values)

Variable	SVL	Age	Sex	Variable	SVL	Age	Sex
BM	0.000	0.812	0.308	RCW	0.003	0.392	0.026
BW	0.000	0.061	0.010	RLST	0.000	0.474	0.018
DCL	0.000	0.233	0.283	RWST	0.008	0.805	0.312
CW	0.000	0.012	0.192	ROL	0.002	0.033	0.007
SL	0.000	0.857	0.167	ROW	0.007	0.203	0.008
SW	0.000	0.480	0.939	RWI	0.292	0.509	0.376
OL	0.000	0.004	0.001	RWN	0.208	0.946	0.060
OW	0.000	0.032	0.004	RPXS	0.632	0.574	0.227
IOW	0.002	0.123	0.548	RLSS	0.058	0.327	0.746
LCR	0.000	0.308	0.347	RWM	0.002	0.367	0.582
WN	0.000	0.841	0.458	RLLMR	0.001	0.667	0.779
PXS	0.005	0.075	0.396				
ML	0.000	0.128	0.173				
LMS	0.000	0.521	0.030				
WSR	0.000	0.020	0.448				
LM	0.000	0.072	0.072				

Minitab procedure: Stat → ANOVA → General Linear Model
Response (dependent variables): morphometric variables
Model (independent variable): *SVL*
Covariates: *Age* and *Sex* for captive non hatchlings

The fact that all age-dependent variables are also size-dependent explains why it is so difficult to predict age of crocodilians based on single variable growth curves (see Section 4.2.2 for discussion). All of the sex-dependent variables are also size dependent, with the exception of RWN. However, its efficiency in predicting individual sex through discriminant analysis is low. Four sex-dependent variables (BW, OL, OW and ROL) are also age-dependent, but the remaining four all of them ratio variables (RCW, RLST, ROW and RWN) are not. Age-dependent as well as sex-dependent variables are primarily located on the cranium. Only one age-dependent (WSR) and sex independent variable is located on the mandible.

Allometric relations of wild animals are presented in Tables 22 - 23 and Figures 9 - 10. Table 22 and Figure 9 show the allometric relations between body and head-size variables and the snout-vent length (SVL). Table 23 and Figure 10 show the allometric relations between ratio variables and SVL. Due to the relatively small sample size, wild males and females are presented together. Table 24 and Figure 11 show the allometric relations between body and head-size variables and the snout vent length (SVL) in captive animals. Table 25 and Figure 12 show the allometric relations between ratio variables and SVL in captive animals.

Table 22. Allometric relations of wild animals' Body- and head-size variables

#	Sex	Y	X	a	b	c	Equation	r^2	N
1	m/f	TTL	SVL	3.5645	1.0825		0.000	0.971	29
2	m/f	SVL	Log BM	363.4319	23.7548		0.000	0.972	29
3	m/f	SVL	BW	9.5225	0.1996		0.000	0.820	29
4	m/f	SVL	DCL	3.7857	0.4816		0.000	0.968	29
5	m/f	SVL	CW	0.1500	0.6596		0.000	0.979	29
6	m/f	SVL	SL	21.6031	-0.3201	0.0174	0.000	0.960	29
7	m/f	SVL	SW	15.3405	-0.0067	0.0189	0.000	0.977	29
8	m/f	SVL	OL	11.8575	2.1830		0.000	0.826	29
9	m/f	SVL	OW	46.1599	5.9175	0.3686	0.000	0.841	29
10	m/f	SVL	IOW	4.5033	4.4825		0.000	0.879	29
11	m/f	SVL	ECR	10.9432	7.0376		0.000	0.883	29
12	m/f	SVL	WN	-2.1679	3.7148		0.000	0.893	29
13	m/f	SVL	PXS	2.1307	2.0340		0.000	0.852	29
14	m/f	SVL	ML	-0.2700	0.3652		0.000	0.969	26
15	m/f	SVL	LMS	1.5657	2.5035		0.000	0.908	29
16	m/f	SVL	WSR	-0.4400	0.7189		0.000	0.960	29

$Y = a + bX + cX^2 + dX^3$

m/f: males and females

Minitab procedure: Stat → Regression → Fitted Line Plot (Polynomial Regression)

With the exception of BM, variables were not transformed because their orders of magnitude were similar and transformation did not improve results.

Cubic element (d) was included in the equation ($d \neq 0$) whenever significant (P-value ≤ 0.05).

Quadratic element (c) was included in the equation ($c \neq 0$) whenever either quadratic or cubic element were significant (P value ≤ 0.05).

With the exception of body mass (BM), log-transformation did not improve the allometric equations for either wild or captive animals. Allometric equations for captive animals presented a higher coefficient of determination (r^2) than the ones for wild animals. Body and head-size variables presented a significantly higher r^2 than ratio variables for both wild and captive animals. They varied from 0.826 (OL) to 0.979 (CW) with body and head-size variables (Table 22), and from 0.002 (RLSS) to 0.581 (RLST) with ratio variables (Table 23) for wild

animals. For captive animals, in their turn they varied from 0.916 (OW) to 0.993 (SW) with body and head-size variables (Table 24) and from 0.003 (RLSS) to 0.534 (RLST) with ratio variables. The range of SVL relative to each equation can be found on the plots of Figures 9 12

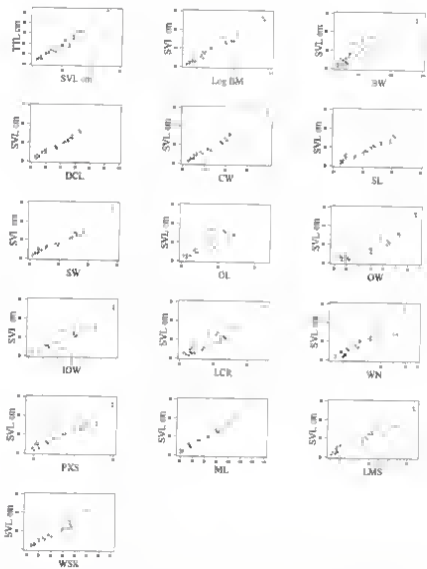


Figure 9 Plots of allometric relations of wild animals Body and head-size variables (Log BM log-transformed BM SVL and TTL in *cm*, the others in *mm*) See Table 22 for regression equations

Table 23 Allometric relations of wild animals Ratio variables

#	Sex	Y	X	a	b	c	d	P-value	r^2	N
1	m/f	SVL	RCW	-66 8226	158 884			0 000	0 370	29
2	m/f	SVL	RLST	7006 83	-522844	1164870	-86021 1	0 000	0 581	29
3	m/f	SVL	RWST	79 0565	-43 1568			0 045	0 140	29
4	m/f	SVL	ROL	96 0670	238 949			0 000	0 523	29
5	m/f	SVL	ROW	14 5130	24 6588			0 323	0 036	29
6	m/f	SVL	RWI	-0 2708	103 195			0 000	0 437	29
7	m/f	SVL	RWN	-2 5876	144 094			0 029	0 164	29
8	m/f	SVL	RPXS	-6 9892	190 882			0 050	0 135	29
9	m/f	SVL	RLSS	24 8324	38 6619			0 805	0 002	29
10	m/f	SVL	RWM	41 2090	21 6420			0 687	0 006	29

$Y = a + bX + cX^2 + dX^3$

m/f males and females

Minitab procedure Stat → Regression → Fitted Line Plot (Polynomial Regression)

Bold the exception of BM variables were not transformed because their orders of magnitude were similar and transformation did not improve results

Cubic element (d) was included in the equation (d ≠ 0) whenever significant (P-value ≤ 0 05)

Quadratic element (c) was included in the equation (c ≠ 0) whenever either quadratic or cubic element were significant (P-value ≤ 0 05)

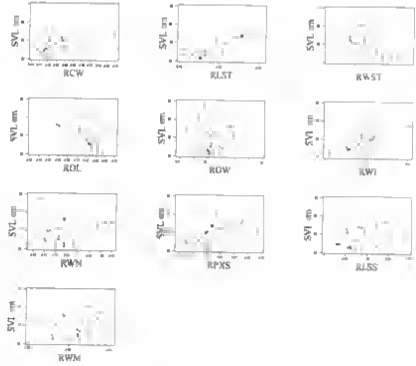


Figure 10 Plots of allometric relations of wild animals Ratio variables See Table 23 for regression equations.

Table 24. Allometric relations of captive non-hatchlings. Body- and head-size variables

#	Sex	Y	X	a	b	c	d	P value	r^2	N
1	m/f	TTL	SVL	1.0876	2.1137	-0.0023		0.000	0.991	120
2	m/f	SVL	LogBM	33.9700	25.1064	8.5085		0.000	0.985	120
3	m	SVL	BW	-1.2780	0.2686	-0.0001		0.000	0.990	25
4	f	SVL	BW	3.4563	0.2078	-0.0004	0.0000004	0.000	0.991	95
5	m/f	SVL	DCL	-0.3508	0.5233			0.000	0.965	120
6	m/f	SVL	CW	-0.5445	0.7817	-0.0010		0.000	0.992	120
7	m/f	SVL	SL	1.4248	0.3152	-0.0009		0.000	0.991	120
8	m/f	SVL	SW	1.7795	0.1650	-0.0006		0.000	0.993	120
9	m	SVL	OL	57.9583	-0.5744	0.1897	-0.0037	0.000	0.982	25
10	f	SVL	OL	33.1170	3.9947	0.2478	-0.0028	0.000	0.970	95
11	m	SVL	OW	31.7964	4.0182			0.000	0.910	25
12	f	SVL	OW	13.1192	3.3430	0.5300	-0.0110	0.000	0.939	95
13	m/f	SVL	IOW	7.5263	4.1475			0.000	0.954	120
14	m/f	SVL	LCR	17.0139	2.4719			0.000	0.981	120
15	m/f	SVL	WN	3.3524	3.4338			0.000	0.974	120
16	m/f	SVL	FXS	-6.9334	2.8570	-0.0137		0.000	0.932	120
17	m/f	SVL	ML	1.0735	0.3818			0.000	0.986	120
18	m/f	SVL	LMS	3.4050	2.9359	0.0098		0.000	0.975	120
19	m/f	SVL	WSR	3.0564	0.8224	0.0011		0.000	0.990	120
20	m/f	SVL	LM	7.2401	0.8567	0.0203	-0.0002	0.000	0.989	98

$Y = a + bX + cX^2 + dX^3$

Sex: m=males, f=females, m/f=males and females

Minitab procedure: Stat → Regression → Fitted Line Plot (Polynomial Regression)

With the exception of BM, variables were not transformed because their orders of magnitude were similar and transformation did not improve results

Cubic element (d) was included in the equation ($d \neq 0$) whenever significant (P-value ≤ 0.05)

Quadratic element (c) was included in the equation ($c \neq 0$) whenever either quadratic or cubic element were significant (P value ≤ 0.05)

Males and females presented separately when ANCOVA for sex was significant (P-value ≤ 0.05). See Table 21 for P values

The coefficients of determination of wild and captive animals concerning body- and head-size variables can be considered extremely high. Their main biological meaning is the apparent lack of morphological variation on the patterns studied, which could be expected for captive but not for wild animals. They also mean that most of the head size variables studied can be useful for predicting body length. This can be particularly interesting for the study of museum collections, or even poaching wastes, in which usually only cranio are preserved or found relatively intact. However, the present study lacks adult wild individuals, which are necessary to increase the range of data in order to include them on future studies.

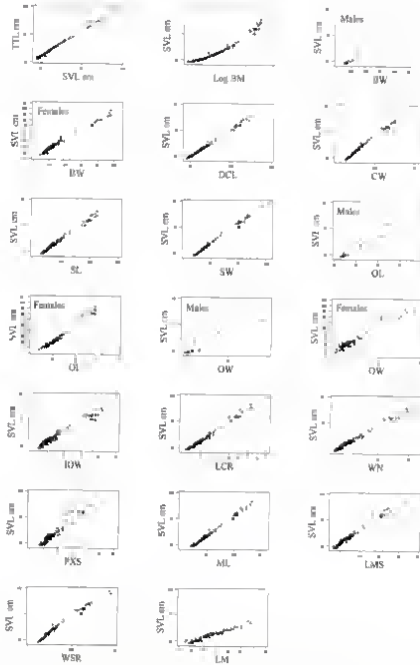


Figure 11 Plots of allometric relations of captive non-hatchlings Body and head size variables. Males and females presented together unless stated otherwise See Table 21 for ANCOVA P values See Table 24 for regression equations.

Table 25 Allometric relations of captive non hatchlings Ratio variables

#	Sex	Y	X	a	b	c	d	P value	r^2	N
1	m	SVL	RCW	214 951	367.644			0 000	0 981	25
2	f	SVL	RCW	8813 67	36715 4	58550 9	22872	0 000	0 839	95
3	m	SVL	RLST	219 636	1106.28	1501 35		0 000	0 934	25
4	f	SVL	RLST	1706 86	18271 9	20270	12759	0 000	0 871	95
5	m/f	SVL	RWST	-4630 87	13095	11943 9	3557 43	0 000	0 452	120
6	m	SVL	ROL	541 144	-3188 86	4835 37		0 000	0 925	25
7	f	SVL	ROL	-569 433	9513 45	-43137 6	60117 3	0 000	0 859	95
8	m	SVL	ROW	126 165	123 61			0 034	0 180	25
9	f	SVL	ROW	26 2212	74 0213			0 534	0 040	95
10	m/f	SVL	RWI	104 269	-869 836	2918 8	7443 13	0 000	0 808	120
11	m	SVL	RWN	-109 85	543 146			0 000	0 674	25
12	f	SVL	RWN	575 858	5780 9	19176 8	19294	0 000	0 818	95
13	m/f	SVL	RPXS	239 553	2197 54	5185 48		0 000	0 118	120
14	m/f	SVL	RLSS	24 3543	108 483			0 565	0 003	120
15	m/f	SVL	RWM	404 504	-1595 72	1691 74		0 000	0 264	120
16	m/f	SVL	RLLMR	56 6440	54 4797			0 068	0 035	98

$Y = a + bX + cX^2 + dX^3$

Sex m=males f=females, m/f=males and females

Minitab procedure: Stat → Regression → Fitted Line Plot (Polynomial Regression)

With the exception of RM variables were not log-transformed because their orders of magnitude were similar and log transformation did not improve results

Cubic element (d) was included in the equation ($d \neq 0$) whenever significant (P-value ≤ 0 05)

Quadratic element (c) was included in the equation ($c \neq 0$) whenever either quadratic or cubic elements were significant (P-value ≤ 0 05).

Males and females presented separately when ANCOVA for sex was significant (P-value ≤ 0 05). See Table 21 for P values

Some precaution is advised when using allometric relations of ratio variables Some of these regression equations are not statistically significant (P-value > 0 100) This is the case for the following variables ROW, RLSS and RWM for wild and ROW and RLSS for captive animals) Plots in Figures 10 – 12 help to visualize these patterns.

Besides helping to estimate body size from head-dimensions the allometric equations above show skull shape changes during the ontogenetic process Non-linear equations express changes on the proportions of the skull –"accelerated" or "decelerated" on the inflexion points For instance, the cranium of captive animals becomes relatively narrower as body size increases (see plot of CW in Figure 11) A similar and expected pattern can be seen on the mandible (see plot of WSR in the same figure) In both cases allometric equations are quadratic with the coefficient of the quadratic element being negative (see Table 24)

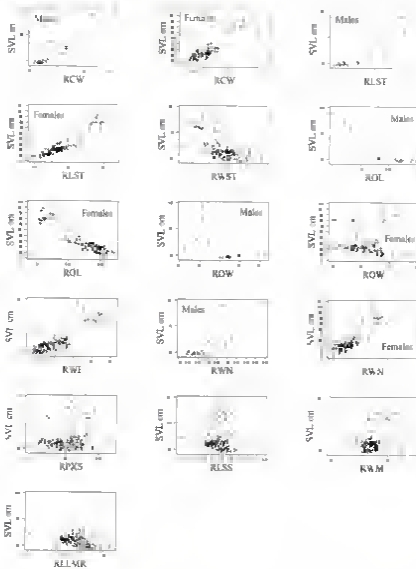


Figure 12 Plots of allometric relations of captive non-hatchlings Ratio variables Males and females presented together unless stated otherwise See Table 21 for ANCOVA P values See Table 25 for regression equations

A somewhat sigmoid shape can be perceived on the allometric growth curve of the eye-orbit length (OL) and width (OW) in captive animals. A positive quadratic and a negative cubic element in the allometric equations of both cases show a period of fast relative growth in young followed by a period of slow relative growth of these regions in adult animals. However, the smaller coefficient of the linear element of the OW equation than of the OL equation expresses the ontogenetic process of "elongation" suffered by the eye-orbits during initial development of the animals. This pattern is compatible with the growth curves of these variables (see Figure 5 and section 4.2.1 for discussion).

4.2.4 Sexual Dimorphism

Sex is phenotypically determined in crocodilians basically by the incubation temperature of their eggs (Bull 1980, Wibbels *et al.*, 1991). However, there seems to be a genetic clutch effect, defined by Lang and Andrews (1994) as the variation in the temperature sex determination (TSD) patterns and responses due the clutch of origin[1]. Female at both lowest and highest, and males at intermediate viable temperatures of incubation (called FMF pattern) seems to be preponderant (Lang and Andrews 1994). *Alligator mississippiensis* (Ferguson and Joanen 1982, 1983) and *Caiman crocodilus* (Lang *et al.* 1989) were initially believe to present FM pattern (females at lower and males at higher temperatures of incubation). However, Lang and Andrews (1994) show that this is incorrect.

Temperature of incubation also affects embryonic development and consequently incubation period (Whitehead *et al.*, 1990). In addition, it may also affect post-hatching growth rates (Joanen *et al.*, 1987 and Webb and Cooper Preston 1989), which is probably related to skin pigmentation and thermoregulatory behavior (Deeming and Ferguson 1989). Besides temperature, the following factors may possibly affect embryo survivorship and post-hatching growth rate: egg size (Getzke and Packard 1985), egg volume and nesting site (Schulte and Chabreck 1990).

How the factors above affect sexual dimorphism is mostly unknown in crocodilians, possibly because crocodilians in general do not present an evident external sexual dimorphism. Direct examination of the genitalia in the cloaca is the method most used to sex these animals (Chabreck 1983, Allstadt and Lang 1995).

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[1] In the section 4.3.2 of the present study, clutch effect is assumed to comprise not only genetic but also environmental effects on the morphometry of eggs and hatchlings due to the clutch of origin.

Although there are some qualitative attempts to describe secondary sexual characteristics in crocodilians (Mellhenny 1935 Vienca 1939 Neill 1971), few multivariate analysis were done in order to quantify such characteristics Using linear discriminant analyses of head measurements and ratios, Webb and Messel (1978) report a proportion of 57 5 to 87% correct sex classification of *Crocodylus porosus* with varying body size (from 40 60 cm SVL to >120 cm SVL, respectively) Hall and Porter (1994) compared two methods of multivariate analysis (discriminant analysis and classification tree analysis), using variables located on the complete skull, cranium and mandible They report results varying from approximately 36 1% to 97.5% of correct classification for the discriminant and from 0 to 100% for the classification tree analysis (the most conservative due to cross validation procedure)

In the present study a multivariate approach is presented in order to quantify sexual dimorphism in wild and captive BSC The questions initially presented (Figure 3) are tested, and the implications of other sources of morphometric variation (e.g., age, clutch, matrilineal lineage, and environment) on sexual dimorphism are discussed.

4 2 4 1 Wild animals

Possibly due to the relatively small sample size and also to the fact that all captured individuals were not adult, sexual dimorphism in wild animals was not clearly detected by Wilk s, Lawley-Hotelling, and Pillai s Tests of MANOVA (P value < 0 100 only for untransformed head-size variables; P value > 0 100 for log-transformed and ratio variables). For this reason subsequent analyses are just made with untransformed head size variables

Linear discriminant analysis of this kind of variable presented a relatively high overall proportion of correct classification (0 724), higher for males (0 800), but significantly lower (0.250) for females (Table 26) This pattern may reflect the male biased distribution of the sample (25 of 29 individuals)

PCA of the same set of untransformed variables (Table 27) showed a considerable amount of variance on PC1 (0 945), with 0 014 due to PC2 This expresses a significant difference between sexes due to overall cranial size. PC1 presents all coefficients with similar magnitude (from 0 265 for OL to 0 283 for DCL and CW) and negative sign

Some "residual" shape change can be interpreted as the contrast between orbital width (OW) and an association between orbital width (OL) and inter orbital width (IOW) These variables present the largest coefficients in absolute value in the second component. Then

inverted sign apparently means a possible widening of the eye-orbit relative to the orbital length and interorbital width

Table 26 Linear discriminant analysis Response sex of wild animals Predictors all head-size variables Sample size 29 animals Groups males and females.

a) Summary of classification with cross-validation

Group	Males	Female
	n	
Males	20	3
Females	5	1
Total N	25	4
N Correct	20	1
Proportion	0 800	0 250

N = 29 N Correct = 21 Proportion Correct = 0 724

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
Males	-166 00	8 73	-26 28	-5 08	12 53	2 81	8 70	13 98	22.71	46 11
Females	-184 83	7.90	-25.20	-8 64	13 14	1 26	13 70	21 34	29 09	53 67

	FXS	ML	LMS	WSR
Males	0.37	0 13	12 12	4 12
Females	2,07	0 12	16 46	2 30

Table 27 Principal components analysis Eigenanalysis of the correlation matrix of all head-size variables Sample size 29 animals Only the six first principal components are presented

Eigenvalue	12.280	0 188	0 163	0 114	0.077	0 061
Proportion	0.945	0 014	0 013	0 009	0 006	0 005
Cumulative	0 945	0 959	0 972	0 980	0 986	0 991
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0 283	0.085	0 048	0 076	0.031	0.240
CW	-0 283	-0 180	-0 085	0 089	0 094	0 033
SL	-0.282	0, 155	0 080	0 135	0.286	0 122
SW	-0 283	-0 058	-0 146	0.217	-0 031	0 149
OL	-0 265	-0 315	0 831	-0 009	-0 190	0 032
OW	-0.276	0.644	0 011	-0 167	-0.273	0.377
IOW	-0.271	-0 384	-0 445	-0 481	-0 063	0 085
LCR	-0.276	0 086	0 115	-0 671	-0 102	0 071
WN	-0 275	-0 383	-0 058	0 111	0 280	-0 762
FXS	-0.277	0 235	-0 074	0.283	-0.269	-0 209
ML	-0 282	-0 023	-0.051	0 141	0 071	0.245
LMS	-0 277	0 220	0 027	-0 066	0 710	0 137
WSR	-0.279	-0 098	-0 221	0.298	-0 342	0.222

Curiously this rearrangement of the orbital region presents the contrary tendency found on growth studies of captive animals (see Table 8 and Section 4 2.2.1 for discussion) Since principal components analysis does not have independent and dependent variables this may not be attributed to sexual dimorphism in this case and ontogenetic change on the former as could be tempting Another possibility is a difference between wild and captive animals (see Section 4 4 2) or the fact that wild animals captured are young only whereas the captive animals sample also includes adult individuals. Allometric relations between OL and OW and SVL in captive animals were represented by cubic equations with a slightly sigmoid shape (Table 24 and Figure 11) This could explain an opposite allometric growth pattern involving young wild and adult captive animals

PC3 shows practically as much variance as PC2 (0 015 and 0 017 respectively) The contrast between OL (-0 800) and IOW (0 527) presented in it may reinforce the idea that the rearrangement of the eye-orbits in the cranium is responsible for most of the shape change in this group Although this may or may not be caused by simple ontogenetic change it is impossible to evaluate how much this pattern is related to sexual dimorphism

Table 28 presents the best subset of head-size variables for sex prediction in wild animals In order to keep the coefficient of determination (r^2) relatively high, only two variables were eliminated from the model (SW and ML) This procedure resulted in a consistent improvement in the results of Wilk s, Lawley Hotelling, and Pillai s Tests of MANOVA (P value=0 032 for all of them) This possibly means that SW and ML insert some "noise" in the model. In other words, these variables introduce some "extra" variance in the system, not related to the morphometric differences between males and females.

Linear discriminant analysis for the best subset of untransformed head size variables (Table 29) shows an improvement on the overall proportion of correct classification (0 828) still higher for males (0 880) than for females (0 500) This improvement of the efficiency of the discriminant analysis corroborates the idea above

PCA of the best subset of variables presents similar results to the analysis run for the whole set of variables, possibly because only two variables were taken off the system (Table 30) PC1 accounts for 0 939 of the total variance, whereas PC2 is responsible for only 0 017 PC1 presents all coefficients with similar magnitudes (0 296 for OW and IOW and 0 309 for DCL and CW) and negative sign

Table 28 Best subset of variables for sexual dimorphism in wild animals

Variables	Best subsets															Evalue	r^2	N
Head-size	DCL	CW	SL	OL	OW	IOW	LCR	WN	PXS	LMS	WSR					0 032	0 636	29

Minitab procedure Stat → Regression → Best subsets
Sample size, 29 animals

Table 29 Linear discriminant analysis. Response: sex of wild animals Predictors Best subset of head-size variables Sample size 29 animals. Groups males and females

a) Summary of classification with cross validation

Group	1	2
1	22	2
2	3	2
Total N	25	4
N Correct	22	2
Proportion	0 880	0 500

N 29 N Correct = 24 Proportion Correct = 0 828

b) Linear discriminant function for group

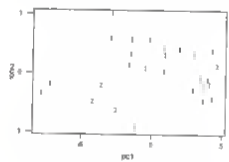
	Constant	DCL	CW	SL	OL	OW	IOW	LCR	WN	PXS
Males	136 53	0 77	-20 95	-4 10	3 96	3.44	3 30	15 32	39 10	-1 17
Females	-152 44	5.84	19 02	2 47	2 46	8 18	10 15	21 57	40 33	0.40

	LMS	WSR
Males	-9 07	7 82
Females	13 28	6.20

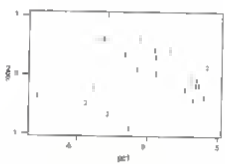
Table 30 Principal components analysis. Eigenanalysis of the correlation matrix of best subset of head-size variables Sample size, 29 animals. Only the six first principal components are presented

Eigenvalue	10.324	0 107	0 160	0 106	0.077	0 056
Proportion	0 939	0 017	0 015	0 010	0 007	0 005
Cumulative	0.939	0 956	0 970	0 980	0 987	0 992
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0 309	0.079	-0 048	-0 085	0 021	0.269
CW	-0 309	-0 179	0 102	-0 136	0.095	0 057
SL	-0 307	0 149	-0 091	-0 130	-0.291	0 193
OL	-0 296	-0 366	-0 880	0 070	0 185	0 035
OW	-0.296	0 033	-0 017	0 143	0 261	-0.464
IOW	-0 296	-0.374	0.527	0.393	0 093	0 120
LCR	0.302	0 061	-0.045	0 675	0 186	-0 015
WN	-0 300	-0 307	0 100	-0 234	-0 305	-0 730
PXS	-0 302	0 236	0 060	-0 380	0 257	0 015
LMS	-0 302	0 220	-0 020	0 058	-0 711	0.223
WSR	-0 304	-0 084	0.210	-0 345	0 344	0.272

Figure 31 shows the plots of wild animals against values for the two principal components. Although there seems to be some differentiation between males and females, there are some consistent "outliers". For a suspicious observer, the first possible explanation for this strange pattern would be a possible mistake on the sexing method used in the field. However, there are other sources of variation in the cranial morphometry of these animals, such as age and area of origin. Thus, it would be prudent to check these possibilities in the other sections of the present study.



a) All head-size variables



b) Best subset of head-size variables

Figure 31. Sexual dimorphism of wild animals. Plots of wild animals' sex against values for the two principal components (1: males, 2: females).

The influence of areas of origin is analyzed in Section 4.4.1. See how animals are clustered in Figure 21 in relation to their sites of origin. Although there is some visible separation between animals from *Dunajlava* (Site 1 in the figure) and the others, their distribution is even less clear than the distribution of males and females on the plots of Figure 13.

Ages of wild animals were estimated through the best subset of variables determined for captive animals (see Figure 8 and Section 4.2.2 for discussion). Although in this case it is still not possible to isolate size effect from age-effect, there is a consensus, although circumstantial evidence that age (possibly interacting with body size) is the major source of variation for wild animals. If true, this introduces a complicating factor in sexual dimorphism studies of crocodilians. In order to isolate sex-effect it is necessary to keep all other things equal: e.g., age, body size, clutch, matrilineal lineage, area of origin, and environment, just to mention the variables analyzed in this study. This is practically impossible in field studies, and very difficult even in captivity, as it is possible to see in the next section.

4.2.4.2 Captive animals

A significant difference between captive males and females was found by MANOVA (P values < 0.000 in Wilk's, Lawley-Hotelling, and Pillai's Tests for the whole set of the three kinds of variables: untransformed and log transformed head-size, and ratio variables). This means that the variance among groups is bigger than the variance intra-group, which answers the first question presented in Figure 3.

In order to evaluate how much individual gender can be predicted, linear discriminant analyses with cross-validation were run for the whole set of untransformed head-size variables (Table 31), log-transformed variables (Table 32), and ratio variables (Table 33). The overall proportion of correct classification varied from 0.816 (untransformed head-size variables) to 0.847 (log-transformed head-size variables), with ratio variables presenting an intermediate result (0.827). Males presented the lower correct classification rate (0.714) with all kinds of variables, where females varied from 0.844 (untransformed variables) to 0.883 (log-transformed variables), with ratio variables again presenting an intermediate rate (0.857).

Principal components analyses of captive animals are presented in the Section 4.2.2.1. See Tables 8, 9, and 10 for PCA of untransformed head-size variables, log-transformed variables, and ratio variables, respectively. The patterns of variation found in the principal components after eigenanalysis are discussed in that section and not repeated here. However, distribution of

males and females in the plots of the two first principal components are presented in Figure 14 at the end of the present section.

Table 31 Linear discriminant analysis Response sex of captive animals Predictors all head size variables. Sample size 98 animals. Groups males and females

a) Summary of classification with cross-validation

Group	1	2
1	15	12
2	3	65
Total N	21	77
N Correct	15	65
Proportion	0.714	0.844

N = 98 N Correct = 80 Proportion Correct = 0.816

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
Males	118.99	2.75	3.42	7.45	1.57	7.09	10.80	6.62	10.72	2.73
Females	123.63	2.82	3.25	8.53	-0.98	7.03	10.03	6.37	11.08	3.09

	PXS	ML	LMS	WSR	LM
Males	0.22	0.07	2.00	-0.47	0.21
Females	0.02	0.11	1.79	-0.96	-0.35

Similar to the pattern showed by wild animals a large number of variables was kept by the best subset regression for captive animals in order to keep a sufficient coefficient of determination (r^2). In other words most of the variables had to be kept in the model in order to account for a reasonable amount of variation. However r^2 was consistently lower for captive animals than for the wild animals (0.636 for the latter and below 0.500 for the former). Twelve untransformed head-size variables (all but DCL and SL), six log-transformed variables (SW, OL, OW, ML, WSR, and LM), and seven ratio variables (RLST, RWST, ROW, RWL, RLSS, RWM, and RLLMR) were kept in their respective sets.

The major source of variation between sexes seem to be small scaled variables (OW and OL). Therefore, log transformation of data significantly improved sexual dimorphism perception through the reduction of scaling-effect among variables. The best subsets of variables (Table 34) showed a consistent difference between sexes for all kinds of variables and criteria tested (P values < 0.000 for Wilk's, Lawley Hotelling, and Pillai's Tests of MANOVA). Linear discriminant analyses with cross-validation for the best subsets of untransformed (Table 35) log-transformed (Table 36) and ratio variables (Table 37) showed a slight improvement on the

overall proportion of correct classifications (0 827, 0 858, and 0 847, respectively). Females still possess a higher proportion of correct classification (0 844, 0 922, and 0 883, respectively) than males (0 762 for untransformed and log transformed variables, and 0 714 for ratio variables).

Table 32 Linear discriminant analysis. Response: sex of captive animals. Predictors: all log-transformed head-size variables. Sample size: 98 animals. Groups: males and females.

a) Summary of classification with cross-validation

Group	1	2
1	15	9
2	6	68
Total N	21	77
N Correct	15	68
Proportion	0 714	0 883

N = 98 N Correct = 83 Proportion Correct = 0 847

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR
Males	-2324 9	5489 9	936 5	2643 8	-1186 4	287 0	521 5	38 7	215.5
Females	2319 1	5466 2	846 0	2625.2	1125 9	247 7	457 1	36.1	211 4

	WN	PXS	ML	LMS	WSK	LM
Males	972 8	35 9	1019 8	-627 4	-937 0	-100 9
Females	972 1	36 4	1035 0	-623 6	-1032 5	158 9

Table 33 Linear discriminant analysis. Response: sex of captive animals. Predictors: all ratio variables. Sample size: 98 animals. Groups: males and females.

a) Summary of classification with cross validation

Group	1	2
1	15	11
2	6	66
Total N	21	77
N Correct	15	66
Proportion	0 714	0 857

N = 98 N Correct = 81 Proportion Correct = 0.827

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS
Males	2686 5	398 9	4994 1	1120 7	4199 7	794 7	447 4	1710 8	42 5
Females	2690 8	-409 6	5038.2	1129 8	4202.8	777 3	439 6	-1721.3	37 3

	RLSS	RWM	RLLMR
Males	973.2	336 2	319 3
Females	1021 1	351 9	261 4

Table 34 Best subsets of variables for sexual dimorphism in captive animals

Variables	Best subsets	P value	r^2	N
Head-size	CW SW OL OW IOW LCR WN PXS ML LMS WSR LM	0 000	0 432	98
Log h-size*	SW OL OW ML WSR LM	0 000	0 455	98
Ratios	RLST RWST ROW RWI RLSS RWM RLLMR	0 000	0 474	98

* Log-transformed head-size variables
Minitab procedure Stat → Regression → Best Subsets

Principal components analyses for the best subsets of variables (Table 38) and their plots (Figure 14) are helpful to visualize how much males and females are clustered apart and also how much other sources of variation may still interfere in these results PC1 is responsible for most of the variation for both the untransformed and the log-transformed head-size variables (0.944 and 0.964 respectively) PC1 coefficients for untransformed variables (see Table 38a) present similar magnitude (from 0 270 for OW to 0.295 to CW and SW) and negative sign PC1 coefficients for log-transformed variables (see Table 38b) are more variable (from 0.204 for OW to 0 476 for SW and ML) although they also present the same sign A possible biological reason for these patterns is that the overall cranium size is the major difference between males and females In addition log transformation may stress these morphometric differences. However these two possibilities are not exactly clarified by the distribution of animals against the values for the two principal components (Figure 14)

Table 35 Linear discriminant analysis Response sex of captive animals Predictors best subset of head-size variables Sample size 98 animals Groups males and females.

a) Summary of classification with cross-validation

Group	1	2
1	16	12
2	5	65
Total N	21	77
N Correct	10	65
Proportion	0 762	0.844

N 98 N Correct = 81 Proportion Correct = 0 827

b) Linear discriminant function for group

	Constant	CW	SW	OL	OW	IOW	LCR	WN	PXS
Males	85 058	-4 092	-1 162	6 168	9 802	0 781	8 787	2 794	-0 871
Females	88 933	-3.904	-0 561	8.921	9.022	0.460	9 142	3.152	-1 073

	ML	LMS	WSR	LM
Males	-0 354	-8 768	0.610	-0.181
Females	-0 322	-8.544	8 132	-0.745

PC2 accounts for 0 019 and 0 018 respectively for untransformed and log-transformed best subset of variables A contrast between OW (-0 811) and the association between OL (0 340) and IOW (0 250) is clear on PC2 of untransformed variables (see PC2 in Table 38a). The contrast is represented by similar magnitudes and opposite signs This is fairly similar to the pattern expressed in Table 8, which is expected since most of the variables were kept in this best subset of untransformed variables The biological meaning of this pattern is discussed in Section 4 2 2 1 and seems to represent a relative "elongation" on the eye-orbits caused by ontogenetic development not exactly by sexual dimorphism

Table 36 Linear discriminant analysis Response sex of captive animals Predictors best subset of log-transformed head-size variables Sample size 98 animals Groups males and females

a) Summary of classification with cross validation

Group	1	2
1	16	6
2	5	71
Total N	21	77
N Correct	16	71
Proportion	0 762	0 922

N = 98 N Correct = 87 Proportion Correct = 0 888

b) Linear discriminant function for group

	Constant	SW	OL	OW	ML	WSR	LM
Males	355 48	-942 65	548 97	444 85	638 02	319 43	-462 32
Females	365 88	-878 54	588 23	421 27	658 24	282 93	519 02

Table 37 Linear discriminant analysis. Response sex of captive animals Predictors best subset of ratio variables. Sample size 98 animals Groups males and females

a) Summary of classification with cross-validation

Group	1	2
1	15	9
2	6	88
Total N	21	77
N Correct	15	88
Proportion	0 714	0 883

N = 98 N Correct = 83 Proportion Correct = 0 847

b) Linear discriminant function for group

	Constant	RLST	RWST	ROW	RWI	RLSS	RWM	RLLMR
Males	-1447 8	2596 7	831 3	484 7	509.3	1067 1	587 0	255 9
Females	-1437 9	2624 9	838 3	385 0	519.5	1111.3	604 9	197 8

Table 38 Principal components analysis of the best subsets of variables for sexual dimorphism of captive animals Sample size 98 animals Only six first principal components are presented

a) Eigenanalysis of the correlation matrix of best subset of head-size variables.

Eigenvalue	11 322	0 224	0 133	0 105	0 058	0.045
Proportion	0 944	0 019	0 011	0 009	0 005	0 004
Cumulative	0.944	0 962	0 973	0 982	0.987	0 991
Variable	PC1	PC2	PC3	PC4	PC5	PC6
CW	-0 295	0 143	0 877	0 084	0 017	0 043
SW	-0 295	0.156	0 098	-0 002	0 092	0 039
OL	-0.284	0 340	0 544	0 025	-0 439	-0 132
OW	-0 270	-0 811	0.235	0 426	-0 125	-0 049
IOW	-0 281	0.250	-0 648	0 556	-0 144	-0 056
LCR	-0 292	0 157	0 148	0 083	-0 162	0 040
WN	0.293	-0 047	-0 165	0 068	0 185	-0 009
FXS	-0 285	-0.214	-0 356	0 558	-0 580	0.255
ML	-0 292	0 046	0 078	-0 046	0 441	0 431
LMS	-0.280	-0 049	-0 059	-0 303	0 208	-0 830
WSR	-0.295	0 132	0 141	-0 007	0 136	0 121
LM	-0.291	-0 155	-0.050	-0 230	0 338	0 137

b) Eigenanalysis of the covariance matrix of best subset of log-transformed head size variables.

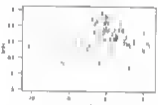
Eigenvalue	0 075797	0 001417	0 000670	0 000342	0 000272	0 000116
Proportion	0 964	0 018	0 009	0 004	0 003	0 001
Cumulative	0 964	0 982	0 991	0 995	0.999	1 000
Variable	PC1	PC2	PC3	PC4	PC5	PC6
SW	-0 476	0.326	-0 247	0 327	-0.310	0.636
OL	-0 309	0.375	-0 174	-0 831	0 206	0 037
OW	-0.204	-0 679	-0 698	-0 067	0 072	-0 006
ML	-0 476	-0 094	0 214	0 316	0 791	-0 038
WSR	-0 451	0 226	-0 134	0 180	-0 337	-0 762
LM	-0 455	-0 490	0.598	-0.256	-0.342	0 109

c) Eigenanalysis of the covariance matrix of best subset of ratio variables

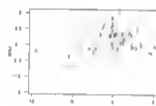
Eigenvalue	0.0095449	0.0048756	0.0022781	0.0009325	0.0007078	0.0002585
Proportion	0 589	0 260	0 122	0 053	0 038	0 013
Cumulative	0 589	0 770	0 891	0 944	0 982	0 995
Variable	PC1	PC2	PC3	PC4	PC5	PC6
RLST	0 341	-0 148	-0 115	-0 008	0 151	0 896
RWST	-0 501	0 600	-0 564	0 090	0 165	0 183
ROW	-0.643	-0 717	-0 170	0 108	-0 127	0 126
RWI	0 442	-0.264	-0 797	-0 073	-0 036	-0 298
RLSS	-0 023	-0 019	-0 009	-0 166	-0 958	-0 151
RWM	-0 070	0 141	-0 053	-0 628	-0 730	0 179
RLLMR	-0 137	-0 120	0 033	-0 744	0 630	-0 058

PC2 of log-transformed variables (see PC2 in Table 38b) shows a more complex pattern of variation, with OW (-0 679) and LM (-0 490) contrasting with SW (0 326), OL (0 375), and WSR (0.226) The biological meaning behind these results seems rather complex, with a possible

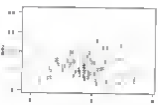
relative elongation in the orbit of the eyes, relative reduction in the toothed region of the mandible, and relative widening of the snout and mandible. This seems to be related to ontogenic development as well.



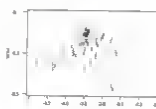
a) All head-size variables



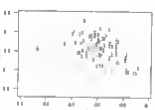
b) Best subset of head-size variables



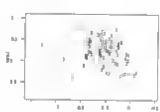
c) All log-transformed head size variables



d) Best subset of log-transformed head-size variables



e) All ratio variables



f) Best subset of ratio variables

Figure 14 Sexual dimorphism of captive animals. Plots of captive animals' sex against values for the two principal components (1 = males, 2 = females).

PCA of ratio variables presented, as expected, a complex result (see Table 38c). PC1 accounts for only approximately half of the total variation, while PC2 accounts for approximately one fourth of it. Contrasts between relative length (RLST) and width (RWST) of snout, and between relative orbital width (ROW) and inter orbital distance (RWI) are showed by PC1

coefficients. Since they are contrasts between non metric width and length variables, they may represent an overall cranium size change, instead of just a local rearrangement of a specific region of the head. ROW (-0.717) accounts for most of the variation of PC2. Since its coefficient has a negative sign, this may represent a relative reduction of this variable, which means again an "elongation" of the eyes' orbits described above.

Figure 14 shows the plots of captive animals against the values for the two principal components for the whole sets and best subsets of untransformed head size variables (Figure 14a and b), log-transformed head-size variables (Figure 14c and d), and ratio variables (Figure 14e and f). Although some separation of males and females can be seen in all plots, it seems to be more clear with log transformed and ratio than with untransformed variables, which is compatible with the results of the discriminant analyses and the best subset regressions.

However, a significant number of apparently misplaced animals is also clear in all plots. Comparing Figure 14 with Figure 7, it is possible to see that there is a considerable influence of age on the distribution of the animals in the plots of the two first principal components. This age effect is increased by the male-biased distribution of one-year old and female-biased distribution of two-year old animals (see Appendix A III and A IV). In addition, age effect cannot be completely isolated from body-size effect (see Table 21).

Tables 3 and 21 shows that there is a consistent sexual dimorphism in BSC. Males and females present distinct growth curves (see Tables 4 - 5 and Figures 5 and 6) and allometric relations (see Tables 24 - 25 and Figures 11 and 12) for a considerable number of variables. It is unlikely that this happens only for captive animals. However, in order to evaluate sexual dimorphism it is necessary to isolate as much as possible other sources of morphometric variation. In this study, age, body size, clutch, matrilineal lineage, site of origin, and environment are superficially analyzed. Other sources of variation, like nutritional and sanitary status of the individuals, geographic region of the population and others, may confound even more the study of secondary sexual characteristics of crocodilians. Apparently, no study so far took all these factors in consideration. Thus, their results may be expressing many different things as "sexual dimorphism".

Since it is practically impossible to keep "all other things being equal" in field studies, experimental design using captive animals may help to solve these problems. Since sex in crocodilians is temperature determined, and there is a considerable clutch effect, an experiment with eggs and hatchlings seems to be the best way to study sexual dimorphism in these animals. For a study like this, clutches should be equally split into *female* and *male* temperatures at

incubation. With this procedure, age, size, and clutch effects would be taken off the system. In addition, extra treatments (for instance, involving hormones, as suggested by Guillette *et al.* 1996a) could be added.

At last, sexual dimorphism studies can be helpful in situations such as the one described by Guillette *et al.* (1996b). Chemical pollutants are apparently affecting the primary sexual characteristics of *Alligator mississippiensis* in Lake Apopka, Florida, with deleterious results for the reproduction rate of the whole population. In this case, the analysis of secondary sexual characteristics of the individuals affected may help to understand how the pollutants impact the population. It may also help to identify the occurrence of similar problems in other areas.

4.3 Parent-offspring Morphometric Relations

Parent-offspring morphometric relations are considered in the present study to be the morphological resemblance between parents and offspring that can be quantified by the use of multivariate morphometric analysis. The main objective of the present study is to investigate biometric relations between parents and offspring that permit the identification of the former by the biometric characteristics of the latter.

The first step will be the study of the allometry of reproduction, where female body weight and length are related with various clutch characteristics such as number of eggs, absolute and relative mass, and egg and hatchlings biometric characteristics (Section 4.3.1). This could be called "allometry of parental investment" (Reiss 1989); however, the concept of parental investment is rather subjective and complex (van Tienhoven 1983). The second step will be the investigation of the morphometric relations between parents and offspring, in such a way that the three questions presented in Figure 3 are tested. For this, clutches, female families, and males will be considered *groups* to which eggs and hatchlings are related (Section 4.3.2).

4.3.1 Allometry of Reproduction

Few studies of the allometry of reproduction have been carried out with crocodilians. Ferguson (1985) presents an extensive review of the reproductive biology and embryology of crocodilians, with information on size at sexual maturity, clutch size, egg dimensions, and biometry of hatchlings for most species. Ferguson's review presents a great amount of information about inter-specific variation on reproductive biology. However, little information is

given about intra-specific variation. In addition, since he depended on literature he had no control on sample size, which for some of the species related resulted in single anecdotal reports.

Hall (1991) used morphometric data from nesting *A. mississippiensis* and *C. novaeguineae* and associated clutch characteristics to produce regression models where demographic profiles of the reproductive females could be reliably estimated on the basis of clutch mass or clutch size. He found consistent allometric relations between female morphometrics (BM, SVL, TTL, and tail girth) and clutch mass and size (r^2 varying from 0.540 to 0.780 and P-value < 0.01 for all equations).

In his elegant study, Hall proposed the study of the allometry of reproduction at the population level, in order to determine which segments or size-classes of females are actively breeding in the population. This seems to be the best approach for large populations, such as the *A. mississippiensis* and *C. novaeguineae*. However, small populations may (and in some circumstances have to) be approached at the individual level. In small fragments of habitat, the "whole segment of reproductive females" may be just one or a few animals. In this case, allometric relations, such as the ones described by Hall may possibly be useful to identify reproductive individuals.

Thorbjarnarson (1996) reviews the reproductive characteristics of crocodilians and presents information on female size, egg mass, clutch size and mass, and some inter- and intraspecific allometric trends. He reports that egg size, clutch size, and clutch mass are positively correlated with female body size at the interspecific level. According to him intraspecific (among populations) comparisons were limited by sample size, but among six species for which data were available, a positive correlation between female size and egg mass was found in all species except *Caiman latirostris*. Thorbjarnarson also reports a significantly positive relationship between clutch mass and female length, but once again *C. latirostris* was an exception. Unfortunately, Thorbjarnarson does not cite his information sources concerning the broad-snouted caiman, which could be useful to clarify these unusual patterns.

In the present study female snout-vent length (SVL) and body mass (BM) are related with the following clutch characteristics: egg mass, length and width, hatchling BM and SVL, and clutch size (number of eggs). Mass, and relative mass (clutch mass / female BM). Relative clutch mass was determined by the ratio between clutch mass and the female BM before reproduction. Data were collected in the captive breeding program of the University of São Paulo, Piracicaba, Brazil, during the reproductive period of 1995 / 1996, with the exception of two nests from former years. Females were measured in early October. At this period of the year

females usually show a small to medium development of follicles (Vaz *et al.*, 1992). Nesting occurs in São Paulo from November to February, with peak in January (Verdade 1995). Least-square regression equations are presented in Table 39. Their relative plots are presented in Figure 15.

Contrary to the pattern described by Thorbjarnarson for BSC, in the present study a positive correlation was found between egg mass and female SVL ($r^2 = 0.699$ and P value < 0.000). A positive correlation, although not so significant, was found between clutch mass and female SVL ($r^2 = 0.405$ and P value = 0.002). Female SVL showed also a significant positive correlation with egg length ($r^2 = 0.548$ and P value < 0.000), egg width ($r^2 = 0.678$ and P-value < 0.000), hatchling BM ($r^2 = 0.627$ and P value < 0.000), and hatchling SVL ($r^2 = 0.619$ and P value < 0.000). No clear correlation was found between female SVL and clutch size ($r^2 = 0.414$ and P value = 0.297). A negative correlation, although not highly significant, was found between female SVL and the relative clutch mass ($r^2 = 0.594$ and P value = 0.065).

Female BM showed a significantly positive correlation with egg mass ($r^2 = 0.693$ and P-value < 0.000), egg length ($r^2 = 0.548$ and P value < 0.000), egg width ($r^2 = 0.582$ and P value < 0.000), hatchling BM ($r^2 = 0.630$ and P-value < 0.000), hatchling SVL ($r^2 = 0.578$ and P-value < 0.000), and clutch mass ($r^2 = 0.615$ and P value < 0.021). No clear correlation was found between female BM and clutch size ($r^2 = 0.354$ and P value = 0.120). A highly significant negative correlation was found between female BM and the relative clutch mass ($r^2 = 0.755$ and P value < 0.005).

With the exception of clutch size, there seems to be a clear positive allometric relation between female body-size (in its turn correlated with BM or SVL) and all studied clutch characteristics, from the egg to the hatchling body-size. In other words, larger females tend to produce heavier (instead of more numerous) offspring. However, this seems to cost relatively less as females grow. For a 20 kg female, the clutch represents approximately 12% of her body mass, whereas for a 40 kg female, the clutch represents only approximately 8%. Not surprisingly, the (negative) correlation between female BM and clutch mass was the most significant allometric relation found in this study ($r^2 = 0.755$).

From the physical constraints suffered by the eggs during incubation to the winter weather conditions faced by hatchlings soon after hatching, there must be a great number of distinct selective pressures (see Campos 1993 and Imhof *et al.*, 1996, for the affect of habitat on the survival of eggs). Although BSC clutch size range shows a variation of approximately 2.72 times from the smallest to the most numerous (18 - 49 eggs, according to Verdade *et al.*, 1992,

approximately the same according to Larriera 1991), there may be a selective pressure strong enough to prevent the viability of smaller clutches

Table 39. Allometry of reproduction: least square regressions

#	Y	X	a	b	c	d	P-value	r^2	N
1	Egg mass (g)	Female SVL (cm)	2211 89	82.3432	-0 9841	0 0039	0 000	0 699	198
2	Egg length" (cm)	Female SVL (cm)	-64 6826	2 55316	-0 0303	0.0001	0 000	0 548	198
3	Egg "width" (cm)	Female SVL (cm)	-70.3161	2.66749	-0.0322	0 0001	0 000	0.678	198
4	Hatchling BM (g)	Female SVL (cm)	-1196 7	45 5406	-0.5536	0 0022	0.000	0.627	124
5	Hatchling SVL (cm)	Female SVL (cm)	-67 8018	3 1135	-0.0399	0 0002	0.000	0.619	124
6	Clutch size	Female SVL (cm)	28 002	0 1515			0.297	0.414	8
7	Clutch mass (kg)	Female SVL (cm)	0 063	0.027			0 002	0.406	8
8	Relative clutch mass	Female SVL (cm)	0 1947	0 0611			0 065	0 594	8
0	Egg mass (g)	Female BM (kg)	96 6885	17.2127	-0 5908	0 0087	0 000	0 693	198
10	Egg "length" (cm)	Female BM (kg)	1 0757	0 5725	-0 0105	0.0002	0 000	0 548	198
11	Egg "width" (cm)	Female BM (kg)	2.3833	0 7046	-0 0241	0 0003	0 000	0 582	198
12	Hatchling BM (g)	Female BM (kg)	66 368	-1 9687	0 0410		0 000	0.638	124
13	Hatchling SVL (cm)	Female BM (kg)	16.5978	-0.3566	0 0061		0.000	0 578	124
14	Clutch size	Female BM (kg)	31 3067	0 3272			0.120	0 354	8
15	Clutch mass (kg)	Female BM (kg)	1 7783	0 8395			0 021	0.615	8
16	Relative clutch mass	Female BM (kg)	0 16	-0 002			0 005	0 755	8

$Y = a + bX + cX^2 + dX^3$
Relative clutch mass: clutch mass (kg) / female BM (kg)
Minitab procedure: Stat → Regression → Regression
Response: Y (see table above)
Predictors: X (see table above)

Hatchling body size may be related to survival rate at the first winter--mainly in the southernmost part of the distribution of the species (Piña *et al.*, 1996). This differential success may benefit larger females. It is tempting to believe that this happens in well established

populations with "healthy" structured age pyramids and a well established hierarchy among reproductive individuals. However this may not be the case of small colonizing populations inhabiting fragmented and anthropogenic habitats, in which social structure and behavioral ecology must be completely altered. The possible consequences for the conservation of the species under such circumstances are unknown

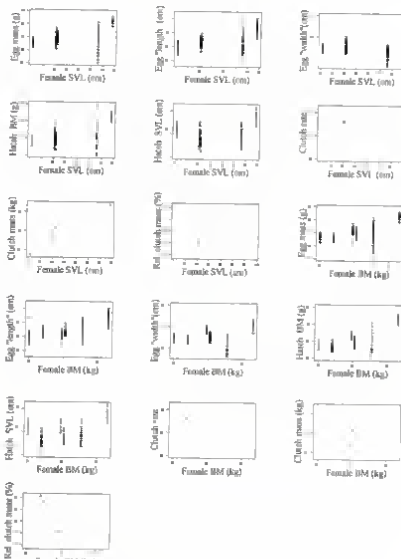


Figure 15. Plots of allometric relations of reproduction. See Table 39 for regression equations. Relative clutch mass (%) = Clutch mass (kg) / Female body mass (kg)

Although the allometric relations above are statistically significant, the high variation found (see Figure 15) prevents their use in the assessment of individual parents from clutch characteristics, even in small populations. In the next section multivariate approaches are attempted in order to accomplish this goal.

4.3.2 Clutch Discrimination

There is a popular concept that a trained chicken farmer can sometimes identify the individual laying hen by the size and shape of an egg. This is considered here a skill that can be developed, quantified, and used for field studies of small populations of crocodilians. The term *clutch discrimination* is used in the present study as the process of distinguishing clutches, based on the morphometry of eggs and hatchlings. Female matrilineal lineage (called here female family) and male effect are evaluated in eggs' and hatchlings' morphometry. Multivariate statistical analysis (as presented in Figure 3) are used here as tools for the evaluation of the differences among groups, reduction in the number of variables, and discriminatory analyses.

Data were collected in the captive breeding program of the University of São Paulo Piracicaba, State of São Paulo, Brazil during the reproductive period of 1995 / 1996. Reproductive groups were formed by a single male with three to five females, three years before the present study, which makes paternity exclusive. Maternity was indicated by maternal behavior during nesting (as described by Colt 1971 for *Crocodylus niloticus*; Hunt 1975 for *C. moreletii*; Bustard 1980 for *Gavialis gangeticus*; Kushlan and Kushlan 1980 for *Alligator mississippiensis*; and Widholzer *et al.* 1986 for *C. latirostris*). PCR primers (developed by Glenn *et al.*– in press– for *A. mississippiensis*) were used in order to establish parentage amongst individuals, but preliminary results showed no exclusion of maternity in most cases. This was possibly due to a high homozygosity between animals.

Six clutches were produced by six nesting females (CL5, CL9, CL10, CL13, CL25, and CL53) and three males (CL1, CL30, and CL203). Females CL5, CL9, CL13, and CL25 are sisters, while the other two females are assumed to be non-related animals. Clutches were produced by the following combination of parents (male/female): #1 (CL203/CL25); #2 (CL30/CL10); #3 (CL1/CL9); #4 (CL30/CL5); #5 (CL203/CL53), and #6 (CL10/CL13). Clutch-effect is defined in this study as the genetic and phenotypic influence of the parents associated with the phenotypic influence of the incubation medium on eggs and hatchlings.

All clutches were collected during the first two days after oviposition. Eggs from all clutches were incubated in vermiculite inside artificial incubators (as described by Verdade *et al.*, 1992b) at the same temperature and relative humidity (31 ± 0.5°C and 90 - 100% respectively). The clutch effect on the morphometry of the eggs is analyzed on section 4.3.2.1. The clutch effect on hatchlings is presented and discussed in section 4.3.2.2. The female-family effect on eggs is presented and discussed in section 4.3.2.3. The female family effect on hatchlings is analyzed in section 4.3.2.4. Males are assumed not to have a significant influence on the eggs' size and shape. Although their effect on hatchlings could not be completely isolated from the female and female-family effect, it is discussed in section 4.3.2.5. Egg morphometry is represented by the following variables: mass (g), "length" (major diameter), and "width" (minor diameter). Hatchlings cranial morphometry is represented by the morphometric variables described in Figure 1 and Table 1. Log-transformation of eggs' measurements is also presented and discussed.

4.3.2.1 Clutch effect on eggs

There is a significant clutch-effect on egg morphometry (P-values < 0.000 for Wilk's, Lawley-Hotelling, and Pillai's Tests of MANOVA) for the whole set of untransformed and log transformed egg measurements. Log transformation did not significantly affect linear discriminant analysis with cross-validation. For both kinds of variables discriminant analysis showed an overall proportion of correct classification of 0.788, varying from 0.564 to 0.975 among clutches for the former (Table 40) and from 0.564 to 0.960 for the later (Table 41).

PCA of anstransformed and log-transformed egg measurements is presented in Table 42. PC1 of untransformed measurements is responsible for 0.851 of the total variation (Table 42a), while PC1 of log transformed measurements accounts for 0.934 (Table 42b). This possibly means that log transformation avidenced a difference in egg overall size between clutches. PC2 of untransformed measurements is responsible for 0.129 of the total variation found, whereas PC2 of log-transformed measurements accounts for only 0.052. This possibly means, in its turn, that log-transformation makes analysis of data less sensitive to changes in egg shape.

Egg mass is the major cause of variation in PC1 for both untransformed and log transformed measurements, followed by egg length in the former and egg width in the later. This suggests that there is a significant variation between clutches in terms of egg mass, which is true (P value < 0.000 in simple ANOVA). PC2 shows a clear contrast between length and width, both

in terms of magnitude (similar) and sign (opposite) for the two kinds of measurements. The relation between these two linear measurements (egg length and width) captures the essence of the egg shape which can be longer or wider but always oval or broadly elliptical. This relation also seems to express an individual female effect. This means that this relation must be the major source of shape variation in the eggs which is explained by the contrast showed in PC2.

Table 40 Linear discriminant analysis. Response: clutch. Predictors: all untransformed measurements. Sample size: 198 eggs. Groups: clutches.

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	29	0	0	2	0	0
CL10	4	24	0	2	0	1
CL9	3	3	22	5	0	0
CL5	2	0	5	18	1	0
CL53	0	0	0	0	39	0
CL13	0	1	0	1	0	24
Total N	38	28	39	28	40	25
N Correct	29	24	22	18	39	24
Proportion	0.763	0.857	0.564	0.643	0.975	0.960

N = 198 N Correct = 158 Proportion Correct = 0.798

b) Linear discriminant function for group

	Constant	Egg mass	Egg length	Egg width
CL25	2394.6	-24.8	278.6	1118.4
CL10	2529.3	-25.0	275.8	1168.5
CL9	-2538.0	-25.8	282.4	1162.3
CL5	2543.9	-25.5	281.4	1101.0
CL53	2660.6	-24.7	277.6	1179.9
CL13	-2597.3	-25.3	268.9	1189.5

However in absolute terms egg mass and egg width seem to be the major sources of overall variation in the eggs form (size and shape). Table 43 presents the best subset regressions of both untransformed and log-transformed egg measurements. In both cases egg mass and egg width are the chosen variables (r^2 varying from 0.569 to 0.574 respectively, with P-value < 0.000 for both cases). The difference between clutches is still significant after the reduction in the number of variables (P-value < 0.000 for Wilk's, Lawley-Hotelling, and Pillai's Tests of MANOVA).

Linear discriminant analysis of the best subset of untransformed (Table 44) and log-transformed measurements (Table 45) showed a slight decrease in the overall proportion of

correct classification (0 707 and 0 702 respectively) in relation to the whole set of measurements (0 788 for both kinds of variables) One of the unrelated females (CL53) and one of the sisters (CL13) kept presenting the highest proportions of correct classifications (above 0 900) similarly to the pattern showed by the discriminant analyses of the whole set of variables The other unrelated female (CL25) showed intermediate results while the other three sisters presented the worst results which is also similar to the pattern formerly presented

Table 41 Linear discriminant analysis Response clutch Predictors all log-transformed measurements (egg mass length and width) Sample size 198 eggs Groups clutches

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	30	1	1	2	0	0
CL10	4	24	9	2	0	1
CL9	2	2	22	5	0	0
CL5	2	0	9	18	1	0
CL53	0	0	0	0	38	0
CL13	0	1	0	1	1	24
Total N	38	28	39	28	40	25
N Correct	30	24	22	18	38	24
Proportion	0 789	0 857	0 564	0 643	0 950	0 960

N = 198 N Correct = 156 Proportion Correct = 0 788

b) Linear discriminant function for group

	Constant	Egg mass	Egg length	Egg width
CL25	3012 6	741 5	1915 5	5018 9
CL10	3050 2	605 2	1874 7	5537 7
CL9	3060 3	591 1	1896 7	5477 9
CL5	3114 6	624 7	1967 9	5661 0
CL53	3386 3	691 3	1940 6	5716 2
CL13	3181 0	952 0	1766 3	5747 4

Squared distance between groups for best subset of variables presented results similar to the whole set of variables, but revealed female CL13 slightly closer to her sisters Females CL5, CL9 and CL10 kept closer to each other than to any other, whereas female CL53 is the most unrelated individual Misclassifications followed this pattern, with the closer sisters showing the highest incidence of misclassification of eggs between each other A possible biological meaning for this pattern is that there must a genetic component on the egg form Another possible reason is the difference of age and body size between related and unrelated females The sisters have similar body size and same age, whereas unrelated females are older and bigger

PCA of the best subset of untransformed and log transformed egg measurements (Table 46) presented approximately equivalent results as shown by the PCA with the whole set of variables PC1 of the untransformed measurements accounted for 0 937 of the total variation (Table 46a) with an equal distribution of this variation between the two variables (0 707 for both egg mass and egg width) However PC1 of the log-transformed measurements accounted for a little more variation (0 972) unequally distributed through the two variables (0 943 for egg-mass and 0 333 for egg width), as can be seen in Table 46b PC2 of untransformed measurements showed an even balance between variables, whereas PC2 of the log transformed variables showed egg width as the major source of variation in counterposition to the pattern of variation expressed on its correspondent first principal component

Table 42 Clutch effect on eggs. Principal components analysis of all measurements Sample size 198 eggs

a) Eigenanalysis of the correlation matrix of all untransformed measurements

Eigenvalue	2 5524	0 3878	0.0599
Proportion	0 851	0 120	0 020
Cumulative	0 851	0 980	1 000
Variable	PC1	PC2	PC3
Egg mass	-0.614	0.050	-0 788
Egg length	-0.552	-0 740	0.383
Egg width	-0 564	0 670	0.482

b) Eigenanalysis of the covariance matrix of all log-transformed measurements

Eigenvalue	0 0026661	0.0001484	0.0000410
Proportion	0 934	0 052	0 014
Cumulative	0 934	0 986	1 000
Variable	PC1	PC2	PC3
Egg mass	-0 889	0 115	0 443
Egg length	-0 338	-0 816	-0 468
Egg width	-0.308	0 566	-0 765

The biological implications of the results above may be interpreted as follows Overall egg size is the major source of variation among clutches Log transformation may stress the role of each variable on the size and shape components of eggs form variation among clutches On the other hand untransformed data seem to be more sensitive to the overall size and shape variation than to the identification of individual variables

Table 43 Best subsets of measurements for clutch effect on eggs

Variables	Best subsets	P value	r	N
Raw measurements	egg mass egg width	0.000	0.569	198
Log-transformed measurements	egg mass egg width	0.000	0.574	198

Minitab procedure Stat → Regression → Best Subsets

Table 44 Linear discriminant analysis Response clutch Predictors. best subset of raw measurements Sample size 198 eggs Groups clutches

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	31	1	2	3	0	0
CL10	0	14	12	3	0	1
CL9	3	9	18	6	0	0
CL5	4	3	7	15	1	0
CL53	0	0	0	0	30	0
CL13	0	1	0	1	1	24
Total N	38	28	39	28	40	25
N Correct	31	14	18	15	30	24
Proportion	0.816	0.500	0.462	0.536	0.950	0.960

N = 198 N Correct = 140 Proportion Correct = 0.707

b) Linear discriminant function for group

	Constant	Egg mass	Egg width
CL25	-1610.9	11.6	973.9
CL10	-1760.9	-12.6	1025.4
CL9	-1732.6	12.4	1015.8
CL5	-1744.6	-12.2	1015.1
CL53	-1882.3	-11.6	1035.9
CL13	-1867.2	-12.6	1050.0

Preston (1953) developed an interesting way to describe shape of bird's eggs, based on the analytical expression of their meridian section or profile reproduced by a "profile-copying machine" developed by himself. This seems to be useful to comparative interspecific studies. However, in intraspecific studies such as this, taking two or three measurements of eggs seems to be less time-consuming and precise enough to capture morphometric variation to reliably discriminate clutches.

Figure 16 shows the plots of eggs against values for the two principal components for the whole set and best subset of untransformed measurements (Figure 16a and b, respectively) and the whole set and best subset of log-transformed measurements (Figure 16c and d). It is possible to see that clutches #1 and #5 and partially #6 are clustered apart from the others. Unrelated females are responsible for clutches #1 and #5 which explains this pattern. Clutch #6 belongs to

one of the sisters that seems to be more distant from the others as was expressed by the squared distances of the discriminant analyses. Clutches #2..#3 and #4 however seemed to belong to the same group. In the next section, female family effect on eggs are discussed. Figure 17 stresses this effect and should be compared with Figure 16.

Table 45. Linear discriminant analysis. Response: clutch. Predictors: best subset of log-transformed measurements. Sample size: 198 eggs. Groups: clutches.

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	30	1	2	3	0	0
CL10	0	15	12	3	0	1
CL9	4	8	18	6	0	0
CL5	4	3	7	15	1	0
CL53	0	0	0	0	38	1
CL13	0	1	0	1	1	23
Total N	38	28	39	28	40	25
N Correct	30	15	18	15	38	23
Proportion	0.789	0.536	0.462	0.536	0.950	0.920

N = 198 N Correct = 139 Proportion Correct = 0.702

b) Linear discriminant function for group

	Constant	Egg mass	Egg width
CL25	-2869.2	1696.0	4287.2
CL10	-2913.4	1537.4	4823.9
CL9	-2906.7	1569.0	4721.4
CL5	-2963.8	1603.3	4712.3
CL53	-3238.8	1659.3	4975.1
CL13	-3060.2	1530.3	5074.9

The plot on Figure 16b shows that log transformation slightly decreases the efficiency of clutch discrimination for female CL53, which is compatible with the results of discriminant analyses. This female's eggs are clearly separated from all the others basically by size. Graphically this can be visualized by the fact that they can be put apart along PC1-axis only. Eggs from female CL25 (clutch #1) seemed to present a consistent difference in shape in relation to the others as can be seen by the preponderance of PC2-axis in their separation from the others. A consistent difference in egg shape seems to separate female CL13 (clutch #6) from her sisters.

Considering that crocodilians seem to present a low genetic variability (Gartside *et al.*, 1977; Adams *et al.*, 1980; Lawson *et al.*, 1989), the results above are highly surprising and promising. Even in a small group of related females, there seems to be enough morphological

variability to discriminate clutches with significant success It is interesting to compare these results with the ones presented in the next sections (4 3 2 2 - 4.3.2 5)

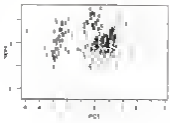
Table 46 Clutch-effect on eggs Principal components analyses of best subsets of measurements. Sample size 198 eggs

a) Eigenanalysis of the correlation matrix of best subset of raw measurements.

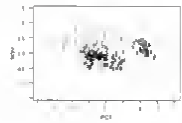
Eigenvalue	1 8741	0 1259
Proportion	0 937	0 063
Cumulative	0 937	1 000
Variable	PC1	PC2
Egg M	0 707	0 707
Egg W	0 707	-0 707

b) Eigenanalysis of the covariance matrix of best subset of log-transformed measurements

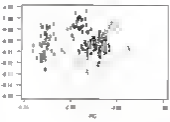
E genvalue	0.0023751	0 0000634
Proportion	0 972	0 028
Cumulative	0 972	1 000
Variable	PC1	PC2
Egg-M	0 943	-0 333
Egg W	0 333	0 943



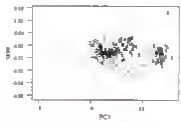
a) All raw measurements



b) Best subset of raw measurements



c) All log-transformed measurements



d) Best subset of log transformed measurements

Figure 16 Clutch effect on the eggs Plots of eggs against values for the two principal components Clutches (male/female) #1 (CL203/CL25) #2 (CL30/CL10), #3 (CL1/CL9), #4 (CL30/CL5), #5 (CL203/CL53), and #6 (CL10/CL13)

4.3.2.2 Female-family effect on eggs

As described above four of the six reproductive females are sisters while the other two are non related individuals Therefore the following female families are recognized in the present study Family #1 (CL25), Family #2 (CL5 CL9 CL10 and CL13), and Family #3 (CL53) These matrilineal lineages also called here female-families are considered here as groups, and their influence on eggs morphometry is analyzed according to the methodology presented in Figure 3 and described early in the text (see Section 3.3)

A significant difference between female families in terms of eggs morphometry was found (P-values < 0 000 for Wilk s, Lawley Hotelling and Pillai s Tests of MANOVA) for the whole set of untransformed and log-transformed measurements Linear discriminant analysis with cross-validation showed significant higher proportion of correct classifications for both untransformed (Table 47) and log-transformed (Table 48) measurements (0 944 and 0 949 respectively) when compared to the clutch effect described in Section 4 3 2 1

Table 47 Linear discriminant analysis Response female/family effect on eggs Predictor all raw measurements Sample size 198 eggs Groups female families

a) Summary of classification with cross-validation

Group	1	2	3
1	34	6	8
2	4	113	8
3	0	1	48
Total N	38	120	40
N Correct	34	113	40
Proportion	0 895	0 942	1 000

N = 198 N Correct = 187 Proportion Correct = 0 944

b) Linear discriminant function for group

	Constant	Egg mass	Egg length	Egg width
1	-2332 8	25 3	310 4	1061 4
2	-2473 1	27 2	313 7	1104 8
3	2555 7	26 5	316 7	1107 6

Consistently to the patterns suggested by clutch effect analyses, families #1 and #2 can be considered closer to each other than family #3 Females CL25 and CL53 (Families # 1 and #3 respectively) seem to be the most unrelated individuals while the group of sisters (Family #2) seem to be in an intermediate position The Regional Studbook of BSC in Brazil is relatively recent (see Verdade and Santiago 1991) Consequently, there is no reliable information about

animals older than five to ten years of age. It is assumed in the present study that females CL25 or CL53 are not related to the females of family #2. They (CL25 and CL53) do not seem to be related to each other as well.

PCA of the whole set of untransformed and log-transformed egg measurements were presented and discussed in the former section (Figure 43). Table 49 shows the best subset regression for the female-family effect on eggs. Their results are consistent with the ones showed by the best subset of measurements for clutch effect analyses (see Table 18), with expectable higher coefficients of determination (r^2).

Table 48. Linear discriminant analysis. Response: female family effect on eggs. Predictor: all log transformed measurements. Sample size: 198 eggs. Groups: female-families.

a) Summary of classification with cross validation

Group	1	2	3
1	34	8	0
2	4	114	0
3	0	8	40
Total N	38	120	40
N Correct	34	114	40
Proportion	0.895	0.950	1.000

N = 198 N Correct = 188 Proportion Correct = 0.949

b) Linear discriminant function for group

	Constant	Egg mass	Egg length	Egg width
1	-2567.8	291.9	2731.9	3818.3
2	2823.1	144.4	2790.3	4263.8
3	2866.6	251.3	2871.2	4369.9

After reducing the number of variables, there is still a significantly difference between female families in relation to egg morphometry, as could be expected (P-values < 0.000 for Wilk's, Lawley-Hotelling and Pillai's Tests of MANOVA for the best subsets of mesurements). Linear discriminant analyses with cross-validation for the best subsets of untransformed (Table 50) and log-transformed measurements (Table 51) showed a slight decrease in the proportion of correct classifications (0.939 to the former and 0.934 to the later). Discriminant analyses of the best subsets also showed similar patterns of distances between female families to the ones showed by the whole set of measurements.

Figure 17 shows the plots of eggs against values for the two principal components for the whole set and best subset of untransformed and log-transformed measurements. Comparing this

with Figure 16 to the former section it is clear the stronger female-family effect in relation to the clutch effect in eggs morphometry Once again it is possible to see that the eggs from female CL53 (i e. Family #3) are clustered apart from the others basically by size differences (i.e., a difference expressed basically by the first principal component) whereas the eggs from female CL25 (Family #1) presents size and shape differences in relation to the others (i e., their variation is spread over PC1 and PC2 axis) Here it is possible to see that Family #2 is at an intermediate position between the unrelated females Log transformation did not significantly improve data analysis Reducing the number of measurements, in its turn did not cause any significant loss of efficiency on the analyses as well

Table 49 Best subsets of measurements for female-family effect on eggs

Variables	Best subsets	P-value	r^2	N
Raw measurements	egg mass egg width	0 000	0 648	198
Log-transformed measurements	egg mass, egg width	0 000	0 647	198

Minitab procedure Stat → Regression → Best Subsets

Table 50 Linear discriminant analysis Response female-family affect on eggs Predictor best subset of untransformed measurements Sample size: 198 eggs. Groups female-families

a) Summary of classification with cross validation

Group	1	2	3
1	34	7	0
2	4	112	8
3	0	1	40
Total N	38	120	40
N Correct	34	112	40
Proportion	0 895	0 933	1 000

N = 198 N Correct = 186 Proportion Correct = 0 939

b) Linear discriminant function for group

	Constant	Egg mass	Egg width
1	-1138 0	9 8	713 2
2	-1253 9	10 5	752 5
3	-1316 5	9 6	752 1

Differences between female families may possibly express a genetic factor related to matrilineal lineage In this case, in situations when a small group of family-related animals inhabit small fragments of habitats--niches from different families may possibly be discriminated with high efficiency Alternatively a change in the pattern of egg morphometry could be related to dispersal or displacement of established reproductive females In these cases,

clutch discrimination based on female and female-family effect on the morphometry of the eggs might be a helpful technique to understand population structure and meta-population dynamics

Table 5.1 Linear discriminant analysis. Response: female-family effect on eggs. Predictor: best subset of log-transformed measurements (egg mass and width). Sample size: 190 eggs. Groups: female families.

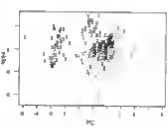
a) Summary of classification with cross validation

Group	1	2	3
1	34	7	0
2	4	111	0
3	0	2	40
Total N	38	120	40
N Correct	34	111	40
Proportion	0.895	0.925	1.000

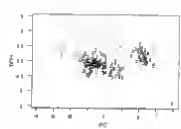
N = 190 N Correct = 185 Proportion Correct = 0.934

b) Linear discriminant function for group

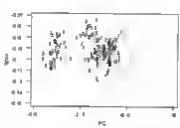
	Constant	Egg mass	Egg width
1	2209.1	1840.9	1708.9
2	2248.9	1726.4	2109.1
3	2470.4	1829.2	2152.9



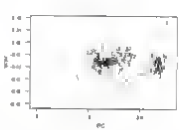
a) All raw measurements



b) Best subset of raw measurements



c) All log transformed measurements



d) Best subset of log-transformed measurements

Figure 17 Female-family effect on eggs. Plots of eggs against values for the two principal components. Families: #1 (CL25) #2 (CL5 CL9 CL10 CL13); #3 (CL53)

4.3.2.3 Clutch affect on hatchlings

There is a significant clutch effect on the cranial morphometry of hatchlings (P values < 0.000 for Wilk s Lawley Hotelling, and Pillai s Tests of MANOVA) for the whole set of untransformed and log-transformed head size variables and ratio variables. The covariance between hatchlings' body length and clutch is presented by head-size and ratio variables in Table 52. Significant differences in ANCOVA mean that clutches present significant differences in the allometric relation between SVL and the morphometric variable in question. The biological meaning for this is a significant difference in hatchlings cranial shape between clutches.

Six of fourteen head-size variables (CW, OL, OW, IOW, ML and WSR) and four of eleven ratio variables (RCW, ROL, RWI and RWM) showed a significant difference between clutches as covariates of SVL. This difference seems to be equally distributed between cranium and mandible, which possibly means that the whole composition of the skull varies among clutches. However, there seems to be a predominance of width variables (CW, OW, IOW, WSR, RCW, RWI, and RWM) over length variables (OL, ML and ROL). This means that hatchlings from different clutches, presenting similar body size, tend to vary more in terms of their relative skull-width than that of their relative skull-length.

Table 52. Analysis of covariance: Clutch as covariate of SVL (P values).

Variable	SVL	Clutch	Variable	SVL	Clutch
DCL	0.000	0.574	RCW	0.194	0.002
CW	0.000	0.010	RLST	0.071	0.441
SL	0.034	0.377	RWST	0.229	0.276
SW	0.002	0.713	ROL	0.059	0.007
OL	0.005	0.000	ROW	0.328	0.552
OW	0.350	0.074	RWI	0.762	0.011
IOW	0.892	0.005	RWN	0.185	0.566
LCR	0.030	0.229	RPXS	0.919	0.919
WN	0.001	0.531	RLSS	0.123	0.985
PXS	0.382	0.774	RWM	0.538	0.000
ML	0.000	0.035	RLLMR	0.378	0.179
LMS	0.000	0.492			
WSR	0.012	0.004			
LM	0.000	0.758			

Minitab procedure: Stat → ANOVA → General Linear Model
Response (dependent variables): morphometric variables
Model (independent variable): *SVL*
Covariates: *Clutch* for captive hatchlings

Since all clutches experienced similar environmental conditions during incubation period the inter-clutch variation found is assumed to come direct from their parents Although, parents nutritional and sanitary status -- to relate a few -- may in theory influence the cranial morphometry of hatchlings, a substantial amount of this variation may be assumed to be genetic In the wild, however, a consistent variation in nesting sites and nest physical conditions is likely to happen, possibly increasing this variation even more

Log-transformation did not affect the results of the linear discriminant analysis with cross-validation (see Tables 53 and 54) The whole set of both untransformed and log-transformed head-size variables presented the same overall proportion of correct classification (0 887), varying from 0 750 (Clutch #2, Female CL10) to 1 000 (Clutch #5, Female CL53) These results are even higher than the ones obtained by the whole set of both untransformed and log-transformed egg measurements (0 788) Ratio variables presented a slightly lower overall proportion of correct classification (0 831) varying from 0 708 to 0.952 respectively to the same clutches above (Table 55)

Squared distances between groups based on hatchlings cranial morphometry showed a slightly different pattern than the one showed by eggs' morphometry Clutch #1 (Female CL25) was the most distant while Clutch #2 (Female CL10) was the closest to the others for all kinds of variables. Log transformation of data resulted in the approximation of Clutch #5 (Female CL53) to the others, which did not happen with untransformed variables Misclassifications predominantly involved clutches from related females, similarly to what happened with eggs

PCA of the whole set of untransformed (Table 56) and log-transformed head-size variables (Table 57) showed similar results PC1 responded for less than half of the total variation (0 463 for the former and 0 411 for the later), whereas PC2 accounted for 14% (0 014) for the former and 22 4% (0 224) for the later The remaining principal components were responsible for 39 7% (0 397) and 36 5% (0 365) respectively for untransformed and log-transformed variables. This means that most of the variation among clutches is expressed by differences in cranial shape not size

PC1 coefficients varied from -0 101 (IOW) to -0 362 (ML) for untransformed variables, and from -0 049 (FXS) to -0 552 (IOW) for log-transformed variables This difference of the weight of IOW in both cases is possibly due to differences in scaling caused by log transformation of data In both cases, PC1 coefficients are more variable than the ones found in age (Section 4.2 2) and sexual dimorphism (4 2 4) studies In these cases overall differences in size were the major source of variation, which is not the case here. PC2 coefficients varied from

0 028 (ML) to 0 498 (WSR) for untransformed variables and from 0 092 (OW) to 0 769 (IOW) for log transformed variables, in absolute values Contrasts of complex biological interpretation are found in shape components of untransformed data, whereas a clear contrast between IOW and all the other variables is presented in PC2 of log-transformed variables

Table 53 Linear discriminant analysis Response clutch effect on hatchling Predictor all head size variables Sample size 124 hatchlings Groups, clutches.

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	20	0	0	0	0	0
CL10	0	18	4	1	0	1
CL9	0	3	24	1	0	0
CL5	1	0	0	12	0	0
CL53	0	0	0	0	21	0
CL13	0	3	0	0	0	8
Total N	27	24	28	14	21	10
N Correct	20	18	24	12	21	9
Proportion	0 963	0 750	0.857	0 857	1 000	0 900

N = 124 N Correct = 110 Proportion Correct = 0.887

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN	PXS
CL25	-1567 7	35 8	3 1	10.5	19 0	40 1	20 9	18 *	47 0	37 0	16 0
CL10	-1733 1	32 8	3 9	-4 0	22 0	52.0	39 1	22 7	54 3	31 7	13 *
CL9	-1988.5	32 1	5.6	1 0	23 0	54 3	36 9	24.2	53 0	29 0	18 1
CL5	1623 3	30.4	4 7	5.2	21 0	53 2	36 3	38 3	53.2	32 3	13 9
CL53	-1930 7	33 3	8 4	-2.8	-24 0	59 9	35 9	25 5	55 7	39 1	13.5
CL13	-1759 6	33 1	-0 0	-6.2	-20 0	57.8	30.0	17 5	52 7	32 8	12 1

	ML	LMS	WSR	LM
CL25	24 4	19 7	3 9	-13 *
CL10	24 0	14 4	3.6	-14 5
CL9	25 0	7 1	3 0	-18.0
CL5	23 5	18.3	1 2	15 0
CL53	28 3	18.8	-0 5	-20 0
CL13	27 4	23.0	1 0	-14.9

Table 54 Linear discriminant analysis Response clutch effect on hatchling Predictor all log-transformed head size variables Sample size 124 hatchlings. Groups clutches

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	26	0	0	0	0	0
CL10	0	18	4	1	0	1
CL9	0	3	24	1	8	0
CL5	1	0	0	12	0	0
CL53	0	8	0	0	21	0
CL13	0	3	0	0	0	9
Total N	27	24	28	14	21	9
N Correct	28	18	24	12	21	9
Proportion	0 963	0 750	0 857	0 857	1 000	0 900

N = 124 N Correct = 110 Proportion Correct = 0 887

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
CL25	18587	16756	259	2405	2043	1872	189	544	1887	-648
CL10	18918	16524	-251	2238	2143	2220	43	523	2009	-705
CL9	18823	16478	-170	2182	2201	2265	4	515	1999	738
CL5	18423	16333	285	2266	2131	2239	42	454	1972	-698
CL53	19045	16580	58	2219	2222	2399	16	511	2041	-628
CL13	18996	16551	-474	2291	2097	2359	0	554	1962	-692

	PXS	ML	LMS	WSR	LM
CL25	-470	11616	1758	361	2288
CL10	-504	11535	1820	360	2237
CL9	-443	11678	1909	334	2375
CL5	-506	11547	1769	249	2254
CL53	-506	11912	1791	188	2444
CL13	-529	11862	1720	242	2255

PCA of ratio variables presented a complex pattern of results (Table 58). PC1 was responsible for 0 689 of the total variation, surprisingly higher than PC1 of non ratio variables, whereas PC2 accounted for 0 095, and the remaining principal components responded for 0 216 of the total variation RWST (-0 968) was the major source of variation on PC1, whereas ROW (-0 953) accounted for most of the variation expressed by PC2 These are rather complex patterns considering that neither RWST nor ROW are size-dependent variables in hatchlings (see Table 52) They may be related, however to the tendency of variation between hatchlings from different clutches, expressed above, in which relative width of head seem to be more important than relative length

Table 55 Linear discriminant analysis Response clutch effect on hatchlings Predictor all ratio variables Sample size 124 hatchlings Groups clutches

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	24	0	0	0	0	0
CL10	2	17	4	1	0	1
CL9	0	4	21	0	1	0
CL5	1	1	0	12	0	0
CL53	0	1	2	0	20	0
CL13	0	1	1	1	0	9
Total N	27	24	28	14	21	10
N Correct	24	17	21	12	20	9
Proportion	0 889	0 708	0 750	0 857	0 952	0 900

N = 124 N Correct = 103 Proportion Correct = 0 831

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS
CL25	-4032 0	850 2	4907 6	755 1	5131.5	1429.2	859 3	-1070 1	728 4
CL10	-4206 0	826 1	5060 3	733 0	5651.2	1515 7	869 0	-1249 0	594 9
CL9	-4153 3	826 0	5031 4	708.1	5763 3	1531.5	872 6	-1305.3	714 5
CL5	-4278 3	825 0	4960 7	726 6	5858 4	1530 4	1025.4	-1217 4	590 6
CL53	-4130 6	930 5	4996.2	717.5	5734 4	1492 2	872.8	-1132 5	531 5
CL13	-4174 9	724 1	5080 9	759.9	5802.3	1521 1	824 1	-1217.2	563.3

	RLSS	RWM	RLLMR
CL25	3542 2	875 2	2209 6
CL10	3359 3	893 6	2241 6
CL9	3167 8	909 4	2130.4
CL5	3549 0	837 4	2222.5
CL53	3466.3	787 0	2186 1
CL13	3596 4	775.2	2207 3

Table 59 shows the best subset of variables for the study of clutch effect Log-transformation did not result in a "best subset" of different variables. Log-transformation did not significantly increase the coefficient of determination (r^2) of the model either Ratio variables presented the lowest r^2 (0 685 against approximately 0 700 of non-ratio variables) The reduction in the number of variables did not affect the significance of the difference between clutches, in terms of cranial morphometry of hatchlings (P-values < 0 000 for Wilk s, Lawley-Hotelling, and Pillai's Tests of MANOVA) for all kinds of variables.

Table 58 Principal components analysis. Eigenanalysis of the correlation matrix of all head size variables. Sample size 124 hatchlings. Only six first principal components are presented

Eigenvalue	6 4794	1 9594	1 1299	0 9076	0 6510	0 5590
Proportion	0 403	0 140	0 081	0 065	0 049	0 047
Cumulative	0 463	0 603	0 683	0 748	0 798	0 845
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0 359	0 066	0 017	0 137	0 005	-0 079
CW	-0 340	0 145	-0 155	-0 180	-0 137	0 010
SL	0 312	-0 169	-0 234	-0 114	0 059	0 003
SW	-0 310	0 150	0 044	-0 034	-0 425	0 030
OL	-0 311	-0 326	-0 069	-0 091	0 028	-0 086
OW	-0 261	-0 391	0 170	0 077	0 032	-0 106
IOW	-0 101	-0 365	0 313	-0 589	-0 020	0 586
LCR	-0 225	-0 195	-0 251	0 537	0 016	0 393
WN	-0 287	0 095	0 302	0 210	0 057	-0 555
PXS	-0 123	0 301	-0 303	-0 322	0 693	0 077
ML	-0 362	0 028	0 008	-0 088	0 073	-0 095
LMS	-0 181	0 300	0 510	0 107	0 090	0 158
WSR	-0 177	0 498	-0 175	-0 023	-0 355	0 318
LM	-0 220	-0 006	0 455	0 378	0 415	0 118

Table 57 Principal components analysis. Eigenanalysis of the covariance matrix of all log transformed head-size variables. Sample size 124 hatchlings. Only six first principal components are presented

Eigenvalue	0 0044483	0 0024227	0 0011254	0 0006740	0 0004871	0 0003754
Proportion	0 411	0 224	0 104	0 062	0 045	0 035
Cumulative	0 411	0 635	0 739	0 801	0 846	0 881
Variable	PC1	PC2	PC2	PC4	PC5	PC6
DCL	-0 165	-0 173	-0 043	-0 028	-0 066	-0 031
CW	-0 198	0 205	-0 079	0 138	0 054	-0 198
SL	-0 385	-0 202	0 257	0 293	-0 138	-0 012
SW	-0 209	-0 215	-0 158	-0 025	-0 034	-0 435
OL	-0 377	-0 087	0 270	-0 079	0 029	0 124
OW	-0 348	-0 092	0 501	-0 137	-0 012	0 116
IOW	-0 552	0 769	-0 277	0 138	-0 017	-0 040
LCR	-0 144	-0 099	0 189	-0 025	-0 242	-0 104
WN	-0 255	-0 209	-0 293	-0 375	0 735	0 072
PXS	-0 049	-0 218	-0 212	0 673	0 155	0 588
ML	-0 214	-0 177	-0 058	0 020	0 015	0 006
LMS	-0 110	-0 159	-0 494	-0 263	-0 543	0 277
WSR	-0 052	0 228	-0 273	0 290	-0 055	-0 524
LM	-0 150	-0 111	-0 140	-0 321	-0 223	0 242

Linear discriminant analyses with cross-validation of the untransformed (Table 60) and log-transformed head-size variables (Table 61) and ratio variables (Table 62) showed a slight decrease on the overall proportion of correct classifications (approximately 0 800 for the two

former and 0 742 for the later) Therefore the reduction in the number of variables represented a decrease of approximately 10% in the efficiency of the model which may be compensated by the time-saving, depending on the programs needed.

Table 58 Principal components analysis Eigenanalysis of the covariance matrix of all ratio variables Sample size 124 hatchlings Only six first principal components presented

Eigenvalue	0 0085704	0.0011878	0.0007021	0 0006319	0.0005438	0 0002955
Proportion	0 809	0 095	0 061	0 051	0 046	0 024
Cumulative	0 589	0 784	0.845	0 896	0 940	0 963
Variable	PC1	PC2	PC3	PC4	PC5	PC6
RCW	-0 009	0 039	-0 149	0 294	0 489	0.527
RLST	0 169	0 016	-0 010	0 119	0 156	0.225
RWST	-0 960	0 042	0 153	0 112	0 029	0 037
ROL	0 083	0 197	0.273	0 159	0 001	0 418
ROW	0 007	-0 953	0 147	0.215	0 077	0 026
RWI	-0 007	-0 024	0.267	-0.552	0 764	-0 192
RWN	0 038	0 075	0 125	0 108	0 158	0.335
RPXS	-0 011	-0.000	-0 137	0 034	0.094	0 031
RLSS	-0 035	0 009	-0 046	-0 130	-0 064	-0 060
RWM	-0 145	-0 114	-0 891	-0 178	0 179	0 094
RLLMR	0 058	-0 172	0 890	-0 072	-0.374	0 582

Once again, clutches from the unrelated females (CL25 and CL53) presented the best rate of correct classification for all kinds of variables The majority of the misclassified individuals belonged to the related females, which express a consistent female-family effect discussed in the next section (4.3.2.4) In this group, the proportion of correct classification varied from 0 500 to 0 800 for head-size variables (both untransformed and log transformed) and from 0 677 to 0 900 for ratio variables The later showed surprisingly better results for the related females than the head-size variables, but its overall rate of correct classification was lower because of the high misclassification presented by Clutch #5 (Female CL53).

Table 59 Best subsets of variables for clutch effect on hatchlings.

Variables	Best subsets	P-value	r^2	N
Head-size	OL, ML, WSR, LM	0 000	0 703	124
Log-transformed head-size variables	OL, ML, WSR LM	0 000	0 705	124
Ratios	ROL, RWI RWM, RLLMR	0 000	0 085	124

Minitab procedure Stat → Regression → Best Subsets

Table 60 Linear discriminant analysis Response clutch effect on hatchlings Predictors best subset of head-size variables Sample size 124 animals Groups clutches

a) Summary of classification with cross-validation

Group	CL25	CL10	CL9	CL5	CL53	CL13
CL25	25	1	0	1	0	0
CL10	0	16	2	1	0	1
CL9	1	2	22	3	0	0
CL5	1	3	4	7	0	1
CL53	0	0	0	0	21	0
CL13	0	2	0	2	0	8
Total N	27	24	28	14	21	10
N Correct	25	16	22	7	21	8
Proportion	0 926	0 667	0 786	0 500	1 000	0 800

N = 124 N Correct = 99 Proportion Correct = 0 798

b) Linear discriminant function for group

	Constant	OL	ML	WSR	LM
CL25	-1000 0	56 3	33 2	10 2	5 3
CL10	-1111 7	87 0	33 7	8 7	5 0
CL9	-1077 7	67 9	34 0	7 0	2 3
CL5	-1035 0	68 0	32 0	6 5	4 0
CL53	-1268 5	75 0	38 0	5 9	1 4
CL13	-1147 1	72 0	35 5	5 4	4 5

The reduction in the number of variables resulted in some rearrangement on the squared distance between groups Clutches from the unrelated females are still considered the most distant for both untransformed and log transformed variables However a surprising approximation between clutches #3 (Female CL9) and #5 (Female CL53) appears with ratio variables This is compatible with the significant number of misclassifications involving these two clutches in the discriminant analysis of ratio variables

PCA of the best subset of variables (Table 63) presented some differences in relation to the PCA with the whole set of variables The variation contained in PC1 increased for both untransformed (Table 63a) and log-transformed head size variables (Table 63b), but decreased for ratio variables (Table 63c) PC1 here accounts for a little more than half of the total variation of head-size variables in hatchlings (0 541 and 0.564 for untransformed and log transformed variables, respectively) PC2 is responsible for approximately one fourth of it (0 244 for the former and 0 238 for the later), whereas the remaining two principal components together account for approximately one fifth of the total variation in both cases Similar to the results of PCA for the whole set of variables, the results above mean that the major source of variation between hatchlings from different clutches is the shape instead of the overall size of the head

Table 61 Linear discriminant analysis. Response clutch effect on hatchlings Pred ctors. best subset of log-transformed head size variables Sample size 124 animals Groups. clutches.

a) Summary af classificatian with cross validation

Group	CL25	CL10	CL8	CL5	CL53	CL13
CL25	25	1	0	1	0	0
CL10	0	16	2	2	0	1
CL8	1	2	23	2	0	0
CL5	1	3	3	7	0	1
CL53	0	0	0	0	21	0
CL13	0	2	0	2	0	9
Total N	27	24	28	14	21	10
N Correct	25	16	23	7	21	9
Proportion	0 926	0 667	0 821	0 500	1 000	0 900

N = 124 N Correct = 100 Proportian Correct = 0 806

b) Linear discrimmant function for group

	Constant	OL	ML	WSK	LM
CL25	10608	2850	11975	453	-451
CL10	10868	3145	12015	384	-442
CL8	10817	3169	12088	341	573
CL5	10658	3174	11944	281	-472
CL53	11364	3365	12395	260	-601
CL13	10599	3274	12154	231	-484

Table 62 Linear discriminant analysis. Response clutch effect on hatchlings Predictors best subset of ratio variables Sample size 124 animals Groups. clutches.

a) Summary af classificatian with cross validation

Group	CL25	CL10	CL8	CL5	CL53	CL13
CL25	22	2	0	0	0	0
CL10	2	17	2	1	0	0
CL8	2	4	19	0	1	1
CL5	1	0	0	11	3	0
CL53	0	0	6	0	14	0
CL13	0	1	1	2	3	9
Total N	27	24	28	14	21	10
N Correct	22	17	19	11	14	9
Proportion	0 815	0 708	0 679	0 786	0 667	0 900

N = 124 N Correct = 92 Proportion Correct 0 742

b) Linear discriminant function for group

	Constant	ROL	RWI	RWM	RLI.MR
CL25	-1654 9	3753 5	1062 0	1652 8	1792 7
CL10	-1737.6	4029 2	1007 8	1610 0	1821 4
CL9	-1605 6	4090 2	1008 4	1590 6	1718 1
CL5	-1804 8	4203 8	1156 8	1565 9	1816 5
CL53	-1676 2	4182 1	1015 3	1517.6	1692 4
CL13	-1697 4	4145 2	961.0	1584.3	1798 3

Table 63 Clutch effect on hatchlings Principal components analysis of best subsets of variables Sample size 124 animals

a) Eigenanalysis of the correlation matrix of best subset of head size variables.

Eigenvalue	2.1656	0.9774	0.6739	0.1831
Proportion	0.541	0.244	0.168	0.046
Cumulative	0.541	0.786	0.954	1.000
Variable	PC1	PC2	PC3	PC4
OL	-0.534	0.444	0.436	-0.570
ML	-0.633	0.017	0.213	0.744
WSR	-0.298	-0.892	0.135	-0.312
LM	-0.475	0.082	-0.863	-0.155

b) Eigenanalysis of the covariance matrix of best subset of log transformed head size variables

Eigenvalue	0.0012033	0.0005078	0.0003422	0.0000804
Proportion	0.564	0.238	0.160	0.038
Cumulative	0.564	0.802	0.962	1.000
Variable	PC1	PC2	PC3	PC4
OL	-0.785	0.432	0.271	-0.352
ML	-0.401	-0.196	0.096	0.860
WSR	-0.151	-0.810	0.453	0.310
LM	-0.386	0.323	-0.844	0.186

c) Eigenanalysis of the covariance matrix of best subset of ratio variables.

Eigenvalue	0.00059969	0.00042938	0.00045960	0.00018535
Proportion	0.432	0.280	0.285	0.083
Cumulative	0.432	0.713	0.917	1.000
Variable	PC1	PC2	PC3	PC4
ROL	-0.404	-0.023	0.916	-0.014
RWI	-0.034	0.828	0.560	0.004
RWM	0.882	-0.128	0.244	-0.382
RLLMR	0.240	0.546	-0.702	-0.134

Relative head width, in its turn, seems to be the major source of shape variation (see PC2 coefficients for WSR in Table 63a and b and PC1 coefficient for RWM in Table 63c) This is also compatible with the patterns expressed by the allometric relations presented in Table 52 Broad snouted caiman is the crocodilian species with the relatively broadest snout It is, therefore, interesting to learn that there is a considerable intraspecific variation of this feature, even more surprisingly involving hatchlings. Although crocodilians are usually considered generalist predators there seems to be a consistent correlation between skull shape and feeding habits but the intraspecific implications of this correlation have not yet been studied

Figure 18 shows the plots of hatchlings against values for the two principal components of the whole set and the best subset of untransformed (Figure 18a and b) and log transformed

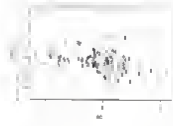
head-size variables (Figure 18c and d) and ratio variables (Figure 18e and f) It is possible to see that clutches (#1 and #5) from unrelated females (CL25 and CL53 respectively) are clustered apart from the others although clutch #3 is also easily identified These patterns are comparable with the results showed by discriminant analyses The female family effect on hatchlings' cranial morphometry is discussed in the next section (4 3 2.4) See Figure 19 to visually compare both clutch and female-family effects

However, the plots present only PC1 and PC2 coefficients which usually represents no more than two thirds of the total variation If new axes were added to the plots of Figure 18 representing the other principal components, the distribution of the clutches would become even more clear However, plots were kept in two dimensions (with only PC1 and PC2-axes) for the sake of simplicity

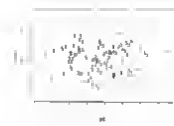
Clutch effect in the cranial morphometry of hatchlings is evident based on the results above Log-transformation of data did not significantly improve the models presented Ratio variables presented again lowest proportions of correct classification in discriminant analysis and complex patterns in PCA Reduction in the number of variables represented a decrease of approximately 10% in the efficiency of the discriminant analyses but it may be useful depending on the precision needed

Clutch affect has been described by Lang and Andrews (1994) to significantly affect the pattern of temperature-sex determination in crocodilians In the present study clutches have been discriminated with approximately 90% of success in an extremely homogeneous group of captive animals with controlled environment of eggs incubation Since female crocodilians build up (or dig) individual nests, clutches are usually isolated from each other in the wild Even nests parasitized by second females usually show separate egg chambers Thus clutch discrimination may result in the assessment of parentage amongst individuals

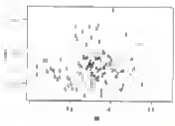
For their originality the results above are extremely significant The establishment of parentage amongst individuals in long-term studies, may be useful for the comprehension of extremely important ecological-behavioral variables such as matrug system and dispersal patterns These variables are intrinsically related to the population structure and meta-population dynamics.



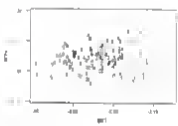
a) All head-size variables



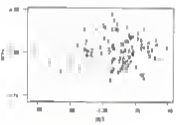
b) Best subset of head-size variables



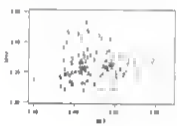
c) All log transformed head-size variables



d) Best subset of log-transformed head-size variables



e) All ratio variables



f) Best subset of ratio variables

Figure 18 Clutch effect on hatchlings Plots of hatchlings against values for the two principal components Clutches (male/female) #1 (CL203/CL25) #2 (CL30/CL10) #3 (CL1/CL9) #4 (CL30/CL5), #5 (CL203/CL53), and #6 (CL10/CL13)

4.3.2 4 Female-family effect on hatchlings

There is a significant female-family effect on the cranial morphometry of hatchlings (P values < 0 000 for Wilk's, Lawley Hotelling and Pillai's Tests of MANOVA) for the whole set of untransformed and log-transformed head size variables, and ratio variables. The covariance between hatchlings cranial morphometry and female-family is presented in Table 64. Significant differences in ANCOVA mean that clutches from different matrilineal lineages present significant differences in the allometric relations between SVL and the morphometric variable in question. The biological meaning for this is a significant difference in hatchlings cranial shape between female-families.

Nine of fourteen head size variables (DCL, CW, SL OL, OW IOW LCR, ML, and LMS) and eight of eleven ratio variables (RCW, RLST, RWST, ROL, RWI, RWN, RPXS and RLSS) showed a significant difference between female families, as covariates of hatchlings' SVL. This is consistently superior to the number of variables influenced by clutch effect itself. However there neither seems to be any predominance of width- or length variable nor a preponderance of the cranium over the mandible. This means that hatchlings from different matrilineal lineages, presenting similar body size tend to consistently vary in skull shape in both relative width and length.

Table 64. Analysis of covariance. Female family as covariate of hatchlings' SVL

Variable	SVL	Female family	Variable	SVL	Female family
DCL	0 000	0 071	RCW	0 194	0 003
CW	0 000	0 000	RLST	0 071	0 000
SL	0 034	0 000	RWST	0 229	0 000
SW	0 002	0.215	ROL	0 059	0 000
OL	0 005	0 000	ROW	0.328	0 346
OW	0 350	0 000	RWI	0 762	0 070
IOW	0 892	0 000	RWN	0 185	0 047
LCR	0 038	0 000	RPXS	0 519	0 080
WN	0 001	0.436	RLSS	0 123	0 007
PXS	0 302	0.262	RWM	0 538	0 338
ML	0 000	0 077	RLLMR	0 378	0.462
LMS	0 000	0 044			
WSR	0 012	0 983			
LM	0 000	0.991			

Minitab procedure: Stat → ANOVA → General Linear Model
Response (dependent variables): morphometric variables
Model (independent variable): *SVL*
Covariates: *Female family* for nativn hatchlings

Linear discriminant analyses with cross-validation for the whole set of both untransformed (Table 65) and log-transformed head-size variables (Table 66) showed the maximum proportion of correct classification (100%) for female-families. Ratio variables (Table 67) presented a rate of 91.1%. Assuming that crocodilians naturally present a low genetic variability, and the group of animals used in this study is extremely homogeneous as these results mean that multivariate analysis may be extremely sensitive to morphometric variation.

Square distances between groups showed a pattern similar to the one presented in the preceding section (4.3.2.3). The group of related females (Family #2) seems to be in an intermediate position in relation to the other unrelated females (Families #1 and #3). The same pattern was found in the analysis of egg morphometry. As seen in the former section intra family variation can be detected as a consistent clutch-effect. However, matrilineal lineage seems to be the major source of variation for the cranial morphometry of hatchlings.

Table 65. Linear discriminant analysis. Response: female-family affect on hatchling. Predictor: all head-size variables. Sample size: 124 hatchlings. Groups: clutches.

a) Summary of classification with cross-validation

Group	1	2	3
1	27	0	0
2	0	76	0
3	0	0	21
Total N	27	76	21
N Correct	27	76	21
Proportion	1.000	1.000	1.000

N = 124 N Correct = 124 Proportion Correct = 1.000

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN	PXS
1	-1323.4	25.7	16.5	-8.7	23.6	37.4	28.6	84.6	46.4	34.6	26.3
2	-1466.4	22.1	17.4	2.4	26.6	50.6	38.1	91.6	52.9	29.2	23.5
3	-1683.0	22.6	23.0	-1.4	-29.2	55.5	37.2	96.5	55.0	37.6	22.0

	ML	LMS	WSR	LM
1	16.4	11.2	2.3	20.4
2	16.5	6.9	-3.2	-21.3
3	18.9	0.7	-6.3	125.3

Principal components analyses of hatchlings were presented and discussed in the former section (4.3.2.3). See Tables 56 - 58 for results. Table 64 shows the best subsets of variables for the analysis of female-family effect on hatchlings. Similarly to the former section--log

transformation did not lead to different subsets of variables However, the best subset for the study of clutch-effect on hatchlings was different from the one chosen for the study of female family Surprisingly however, the coefficients of determination (r^2) of the best subsets of variables for the former were higher than for the later

Table 66 Linear discriminant analysis, Response female-family effect on hatchling Predictor all log-transformed head-size variables Sample size 124 hatchlings Groups clutches

a) Summary of classification with cross-validation

Group	1	2	3
1	27	0	0
2	0	76	0
3	0	0	21
Total N	27	76	21
N Correct	27	76	21
Proportion	1 000	1 000	1 000

N = 124 N Correct = 124 Proportion Correct = 1 000

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN	PXS
1	-13980	13297	2157	-2640	2171	1322	260	991	1451	-624	349
2	-14197	13012	2168	-2479	2268	1086	78	1027	1646	-698	386
3	-14733	13073	2415	-2466	2341	1803	-94	1052	1699	589	-485

	ML	LMS	WSR	LM
1	8649	-1480	960	2468
2	8654	1535	904	2582
3	8836	1580	1122	2649

The reduction in the number of variables (Table 68) did not affect the significance of the difference between female-families for all kinds of variables (P value < 0 000 for Wilk's, Lawley-Hotelling, and Pillai's Tests of MANOVA) Linear discriminant analyses with cross-validation of the best subsets of untransformed (Table 69) and log transformed head size variables (Table 70), and ratio variables (Table 71) showed a slight decrease in the overall proportion of correct classification (0 976 0 976 and 0 823 respectively) Once again log transformation did not improve analysis of data, and ratio variables presented a lower efficiency than head size variables

PCA of the best subsets of variables is presented in Table 72. PC1 is responsible for most of the variation in all cases. It varies from 0 532 for the ratio variables to 0 686 for the log transformed variables, with untransformed variables presenting an intermediate value of 0 625

These PC1 values are significantly higher than the ones presented by the first principal components for the best subsets of variables in the study of clutch effect

Table 67 Linear discriminant analysis Response female-family effect on hatchling Predictor all ratio variables Sample size 124 hatchlings Groups clutches

a) Summary of classification with cross-validation

Group	1	2	3
1	26	1	0
2	1	67	1
3	0	8	20
Total N	27	76	21
N Correct	26	67	26
Proportion	0 963	0 882	0.952

N = 124 N Correct = 113 Proportion Correct = 0 911

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPKS	RLSS
1	-3827 5	663 7	5319 8	726 7	5231 1	1487 3	165 8	1411 5	1233 2	2496 0
2	-4000 4	634.2	5471 1	704 0	5786 2	1577 5	183 7	-1502.2	1096 3	2328 9
3	3951 9	737.0	5433 1	696 5	5735.0	1541 5	163 9	1461 5	984 6	2426 3

	RWM	RLLMR
1	951 0	1802 6
2	960 9	1836 9
3	886 8	1754 0

Table 68 Best subsets of variables for female-family effect on hatchlings

Variables	Best subsets	P value	r^2	N
Head size	CW SL, OL WSR	0 000	0 837	124
Log transformed head-size	CW SL OL, WSR	0 000	0 832	124
Ratios	RLST ROL RWM RLLMR	0 000	0.698	124

Minitab procedure: Stat → Regression → Best Subsets

A possible biological meaning for these results is that overall skull size may be the major source of variation among hatchlings from distinct matrilineal lineages, whereas skull shape seems to be the major variation between clutches of the same female-family Skull size is directly correlated with body size Thus the results above may imply that hatchlings from different matrilineal lineages tend to present consistent variation in body-size. Body size in its turn may be directly related to survival rate of hatchlings during the first winter and consequently to the relative reproductive success of the female Relative reproductive rate in its turn is directly

related to fitness (Krebs 1985 709) Crocodilians present a complex social structure with possible ranking hierarchy among females (Lang 1987) Differential reproductive success may be related to the female social ranking position. Matrilineal lineage could therefore be related to the maintenance of social rank, which could also be related to sex determination, analogously to the pattern described by Simpson and Simpson (1982) for rhesus monkeys.

Table 69 Linear discriminant analysis Response female-family effect on hatchlings Predictors best subset of head-size variables Sample size 124 animals. Groups clutches.

a) Summary of classification with cross-validation

Group	1	2	3
1	26	1	0
2	1	74	0
3	0	1	21
Total N	27	76	21
N Correct	26	74	21
Proportion	0.963	0.974	1.000

N = 124 N Correct = 121 Proportion Correct = 0.976

b) Linear discriminant function for group

	Constant	CW	SL	OL	WSR
1	-715.52	37.07	6.27	58.20	-0.73
2	-806.14	37.25	9.66	66.99	-3.03
3	-954.48	42.82	11.02	72.60	-5.93

Table 70 Linear discriminant analysis Response female family effect on hatchlings Predictors best subset of log-transformed head-size variables Sample size: 124 animals Groups clutches

a) Summary of classification with cross-validation

Group	1	2	3
1	26	1	0
2	1	74	0
3	0	1	21
Total N	27	76	21
N Correct	26	74	21
Proportion	0.963	0.974	1.000

N = 124 N Correct = 121 Proportion Correct = 0.976

b) Linear discriminant function for group

	Constant	CW	SL	OL	WSR
1	-5748.0	6438.4	-63.6	3579.5	-446.6
2	-5954.9	6434.8	20.9	3825.5	547.4
3	-6317.0	6684.8	49.3	3965.7	-668.9

Table 71 Linear discriminant analysis Response female-family effect on hatchlings Predictors best subset of ratio variables. Sample size 124 animals Groups clutches

a) Summary of classification with cross-validation

Group	1	2	3
1	25	3	0
2	2	59	3
3	0	14	18
Total N	27	76	21
N Correct	25	59	18
Proportion	0 926	0 776	0 857

N = 124 N Correct = 102 Proportion Correct = 0.823

b) Linear discriminant function for group

	Constant	RLST	ROL	RWM	RLLMR
1	1861.3	2241 3	3847.2	1545 5	1708 3
2	−1993 0	2403 0	4146 8	1507 0	1732 8
3	1976 0	2434 0	4208 5	1459 6	1663 6

Table 72 Female-family effect on hatchlings Principal components analyses of the best subsets of variables Sample size 124 animals

a) Eigenanalysis of the correlation matrix of best subset of head size variables.

Eigenvalue	2.4989	1 0792	0 2703	0.1516
Proportion	0 625	0.270	0 068	0 038
Cumulative	0 625	0 895	0 962	1.000
Variable	PC1	PC2	PC3	PC4
CW	0 579	0.226	-0.335	0 708
SL	0.548	-0.275	0 790	0 014
OL	0.510	-0 472	-0 509	-0 508
WSR	0.323	0.806	0.066	-0.491

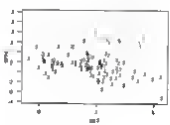
b) Eigenanalysis of the covariance matrix of best subset of log transformed head-size variables

Eigenvalue	0 0019005	0 0005491	0 0002532	0.0000673
Proportion	0 686	0 198	0 091	0 024
Cumulative	0 686	0.884	0 976	1 000
Variable	PC1	PC2	PC3	PC4
Lcw	-0.343	0 388	-0.264	-0 814
Lsl	-0 710	-0.035	0 701	0 056
Lol	-0 599	-0 373	-0 648	0.286
Lwr	-0 135	0 842	-0 137	0.503

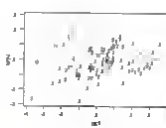
c) Eigenanalysis of the covariance matrix of best subset of ratio variables.

Eigenvalue	0 0010671	0.0005324	0.0002633	0.0001443
Proportion	0 532	0.265	0 131	0 072
Cumulative	0 532	0 797	0 928	1.000
Variable	PC1	PC2	PC3	PC4
RLST	-0 347	-0.230	-0 731	0 541
ROL	-0 402	-0 904	-0 113	-0 017
RWM	0 801	-0.406	-0 395	-0 193
RLLMR	0 276	0 884	-0 374	0 049

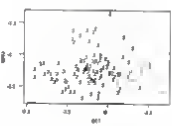
Figure 19 shows the plots of hatchlings against values for the two principal components of the whole set and best subsets of untransformed (plots a, b) and log transformed head-size variables (plots c d), and ratio variables (plots e f) It is possible to see how clustered apart the distinct female families are from each other Once again log-transformation did not improve visualization of results and ratio variables were less efficient than head-size variables. It is interesting to compare these results with clutch-effect in Figure 18 and apparent male-effect on hatchlings showed in Figure 20



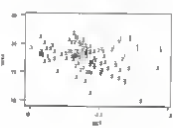
a) All head-size variables



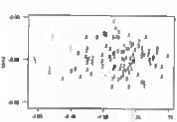
b) Best subset of head-size variables



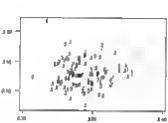
c) All log-transformed head-size variables



d) Best subset of log transformed head-size variables



e) All ratio variables



f) Best subset of ratio variables

Figure 19 Female-family effect on the hatchlings- Plots of hatchlings against values for the two principal components Families #1 (CL25), #2 (CL5 CL9 CL10 CL13) #3 (CL53).

4.3.2.5 Male effect on hatchlings

Males' effect on hatchlings could not be completely isolated from clutch and female family effect because this would require a larger sample size and possibly an experimental design, which was impossible to obtain with the available animals. However, as an exploratory exercise the "apparent" male effect is here presented and discussed. This effect seems to be significant (P value < 0.000 for Wilk's, Lawley Hotelling, and Pillai's Tests of MANOVA). Linear discriminant analyses with cross-validation are presented in Table 73 for the whole set of untransformed head-size variables, in Table 74 for the log-transformed head-size variables, and in Table 75 for ratio variables.

Table 73 Linear discriminant analysis. Response: male effect on hatchling. Predictor: all head-size variables. Sample size: 124 hatchlings. Groups: males.

a) Summary of classification with cross-validation

Group	CL203	CL30	CL1
CL203	40	3	1
CL30	7	41	3
CL1	1	4	24
Total N	48	48	28
N Correct	40	41	24
Proportion	0.833	0.854	0.857

N = 124 N Correct = 105 Proportion Correct = 0.847

b) Linear discriminant function for groups

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
CL203	-876.33	35.20	-7.83	-38.20	-1.41	-22.21	-0.13	52.73	20.25	33.11
CL30	-838.48	33.24	10.92	-38.48	-0.91	19.20	4.45	53.00	22.07	26.80
CL1	-795.42	33.34	9.75	-34.49	2.41	19.09	4.61	51.11	21.26	23.75

	PXS	ML	LMS	WSR	LM
CL203	27.70	0.77	39.07	9.93	3.88
CL30	26.21	5.29	37.75	11.17	6.44
CL1	30.79	5.75	29.43	11.52	3.49

Log-transformation once again did not improve the results of the linear discriminant analysis with cross-validation. The proportions of correct classification varied from 0.831 for ratio variables to 0.847 for both untransformed and log transformed head-size variables, which is still considerably high. Male CL1 is son of the male CL203. However, squared distances between groups show that male CL30, although unrelated, seems to be in an intermediate position between them.

Principal components analyses of hatchlings are presented and discussed in a former section (4.3.2.3). See Tables 56 - 58 for results. Figure 20 shows the plots of hatchlings against values for the two principal components for untransformed (Figure 20a) and log transformed head-size variables (Figure 20b) and ratio variables (Figure 20c). Comparing these plots to the ones presented in Figure 19, it is evident that hatchlings are clustered according to female family and not to the male. In other words, discriminant analysis could not isolate male effect from female-family and clutch effect, resulting in an erroneous interpretation of its results. This mistake can be perceived by the principal components analyses. This shows that male effects on cranial morphometry of hatchlings are consistently less evident than matrilineal lineage. The determination of its actual magnitude would require an experimental design.

Table 74. Linear discriminant analysis. Response: male effect on hatchling. Predictor: all log-transformed head-size variables. Sample size, 124 hatchlings. Groups: males.

a) Summary of classification with cross-validation

Group	CL203	CL30	CL1
CL203	40	3	1
CL30	7	41	3
CL1	1	4	24
Total N	48	48	28
N Correct	40	41	24
Proportion	0.833	0.854	0.857

N = 124 N Correct = 105 Proportion Correct = 0.847

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
CL203	-11367	14982	8	-4138	717	2359	1540	562	-384	-692
CL30	-11168	14828	148	-4893	701	2279	-1458	565	331	762
CL1	-11188	14838	-95	-4043	-749	2279	1454	553	358	-799

	PXS	ML	LMS	WSR	LM
CL203	138	7096	954	238	-699
CL30	-158	6981	1012	287	596
CL1	-92	7018	1113	303	713

4.4 Morphometric Analysis of Wild Animals

The field sites where wild animals were capture for the present study are described in Section 3.4. All of them are located in the East-Central region of São Paulo State, Brazil (Figure 3). They are all connected to subsidiaries of Tietê River - the main river of the State of São Paulo which runs westward and cross almost the whole State. *Volta Grande* and *Porto de Areia* are

marginal wetlands of Piracicaba River one of the main north subsidiaries of Tietê River *Pantanal* is a marginal wetland and *Cherquesada* is an artificial pond both being connected to Azacuá Creek a subsidiary of Piracicaba River These field sites are located no farther than 15 km from each other *Duraflora* is the most distant field site located approximately 150 km far from the others It is a group of artificial ponds connected to Pederneiras Creek, a south subsidiary of Tietê River

Table 75 Linear discriminant analysis Response male effect on hatchling Predictor all ratio variables Sample size 124 hatchlings Groups males

a) Summary of classification with cross-validation

Group	CL203	CL30	CL1
CL203	41	5	1
CL30	6	37	2
CL1	1	6	25
Total N	48	48	28
N Correct	41	37	25
Proportion	0 854	0 771	0 893

N = 124 N Correct = 103 Proportion Correct = 0 831

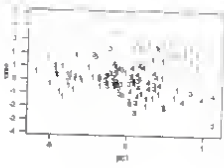
b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS
CL203	-3928 5	508 7	5239.2	900 6	4178 9	1343 5	257 8	-1010 5	959 2
CL30	-4053.3	428.5	5321 7	905 4	4386.2	1394 5	282.3	-1138.9	945 7
CL1	-3975.6	427 5	5290.3	885 2	4376.7	1399.3	265 8	-1193 8	1099.4

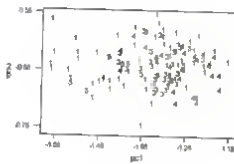
	RLSS	RWM	RLLMR
CL203	3847 4	858.6	2377 9
CL30	3901.2	896 1	2468.3
CL1	3575.7	942 9	2380 1

Studies of morphometric geographic variation involving crocodilians have traditionally been related with taxonomy of similar taxa (Mook 1921b, Freiberg and Leitão de Carvalho 1965 Jordanskiy 1973, Medem 1983, Hall 1989 Monteiro and Soares in press), although some studies have also been related to intraspecific variation (Mook 1921a, Dodson 1975, Webb and Messel 1978 Montague 1982 Aquino 1994 Hall and Portier 1994).

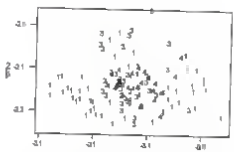
In the present study morphometric analyses of wild animals are carried out with the objective of establishing differences between the subpopulations studied (Section 4 4 1) and also between wild and captive animals (Section 4 4 2) Groups are studied as described in Figure 2



a) All head-size variables



b) All ratio variables



c) All log-transformed variables

Figure 20 Apparent male effect on hatchlings Plot of hatchlings against values for the two principal components. Males #1 (CL203) #3 (CL30) #4 (CL1)

4.4.1 Differences among Subpopulations

There is a significant difference among subpopulations from the areas studied in relation to the cranial morphometry of individuals (P-value < 0.000 for Wilk's, Lawley-Hotelling, and Pillai's Tests MANOVA for all kinds of variables). However, linear discriminant analyses with cross-validation for untransformed (Table 76) and log-transformed head-size variables (Table 77), and ratio variables (Table 78) showed relatively low overall proportion of correct classifications. Log-transformation did not significantly increase model efficiency (0.655 against 0.621 for untransformed data) and ratio variables presented the lowest rate of correct classification (0.483).

The squared distance between groups presented similar patterns independently of the kind of data manipulation (e.g., log-transformation). However, in all cases *Volta Grande* and *Pontunal* were presented as the most distant sites between each other, which does not correspond to their geographic location. In addition, *Porto de Areia* and *Duraflora* were presented as the closest sites between each other, which does not correspond either to their geographic location. Possible reasons for this unexpected pattern are discussed below.

PCA of the whole set of head-size variables is presented and discussed in Section 4.2.4 (see Table 27). PCA of log-transformed head-size variables (Table 79) showed similar patterns, with PC1 as the major source of variation (0.945 for the former and 0.951 for the later). PC2 accounted for approximately 15% of the total variation in both cases. OW and IOW were respectively the major sources of variation in PC2 for the untransformed and log-transformed variables, although the contrast between variables in the later is not as clear as in the former.

PCA for ratio variables (Table 80) showed a distinct pattern, with PC1 accounting for less than half and PC2 for approximately one fourth of the total variation. ROW is the major source of variation in PC1, which seems to be compatible with the patterns showed by PCA for head-size variables. RWST and RWI are the major source of variation in PC2, which possibly represents a contrast between the relative width of snout and the relative inter-orbital length. This contrast is similar to the ones caused by sexual dimorphism, as discussed in Section 4.2.4.1.

Table 81 shows the best subsets of variables for the morphometric analyses of the differences among subpopulations. Width variables predominate in the best subsets of both untransformed and log-transformed head-size variables, whereas length and width variables counterbalance in the best subset of ratio variables. Variables located both in the cranium and mandible are present in the best subsets, which possibly means that differences among subpopulations involve overall size and shape variations in the whole skull of animals.

Table 76 Linear discriminant analysis Response area of origin Predictor all head-size variables Groups study-sites (1 *Volta Grande* 2 *Porto de Areia* 3 *Pontanal* 4 *Charqueada* and 5 *Duraflora*) Sample size 29 animals

a) Summary of classification with cross-validation

Group	2	5	1	3	4
2	0	1	0	2	0
5	2	9	1	0	0
1	0	1	1	0	0
3	1	0	0	1	2
4	0	1	0	0	1
Total N	9	12	2	3	3
N Correct	6	9	1	1	1
Proportion	0.667	0.750	0.500	0.333	0.333

N = 29 N Correct = 18 Proportion Correct = 0.621

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
2	-491.18	17.59	37.23	-28.03	7.29	1.03	22.72	37.44	47.77	82.38
5	-489.64	18.76	36.72	28.04	8.38	-2.80	14.23	32.06	40.90	83.29
1	-375.38	15.37	31.99	23.98	10.12	0.55	22.83	27.92	34.34	73.66
3	-650.44	19.37	-35.81	31.64	3.74	-1.71	24.94	49.09	53.77	95.86
4	-574.80	19.26	-43.20	30.57	7.51	-6.22	20.70	41.34	52.17	99.89

	PXS	ML	LMS	WSR
2	4.79	1.28	-8.84	3.89
5	0.40	1.47	-13.83	-1.33
1	7.25	0.38	-14.97	3.23
3	6.71	1.89	-14.72	-8.25
4	13.21	1.39	-21.83	0.13

A significant difference among subpopulations still persists after reduction in the number of variables (P values < 0.000 for Wilk's, Lawley-Hotelling, and Pillai's Tests of MANOVA) for the best subset of untransformed and log-transformed head-size variables and ratio variables. Linear discriminant analyses with cross validation showed an overall improvement in the rate of correct classifications for the three kinds of variables (Table 82—84).

The squared distance between groups showed a similar pattern for the head-size variables (both untransformed and log-transformed), with *Volta Grande* and *Pontanal* as the most distant sites as before the reduction in the number of variables. However the best subset of ratio variables prescuted these two sites as the closest ones. This paradoxal pattern is possibly related to the small sample size. Individuals age and gender may also influence the results above, since these sources of variation could not be isolated.

Table 77 Linear discriminant analysis Response: area of origin Predictor: all log-transformed head-size variables. Groups: study sites (1 *Volta Grande* 2 *Porto de Areia* 3 *Pontonal* 4 *Charqueada*; and 5 *Duraflora*). Sample size: 29 animals

a) Summary of classification with cross-validation

Group	2	5	1	3	4
2	7	1	0	2	0
5	2	9	1	0	0
1	0	1	1	0	0
3	0	0	0	1	2
4	0	1	0	0	1
Total N	9	12	2	3	3
N Correct	7	9	1	1	1
Proportion	0.778	0.750	0.500	0.333	0.333

N = 29 N Correct = 19 Proportion Correct = 0.655

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR
2	-4023.9	7352.8	7606.6	-3558.0	1681.6	-1301.0	-2432.1	735.6	7963.9
5	-4007.9	7261.2	-7504.4	3415.8	1543.7	1359.3	2700.2	-799.0	8008.2
1	3815.7	7059.4	-6959.9	3290.9	1827.0	1206.2	2389.9	807.4	7516.1
3	-4332.4	7619.3	-7524.1	3719.0	1441.6	-1338.4	2504.2	-649.8	8375.0
4	-4194.8	7575.6	-8091.7	3676.0	1750.1	-1466.3	2495.8	717.1	8230.0

	WN	PXS	ML	LMS	WSR
2	3157.9	573.6	2671.9	3153.3	-713.4
5	3184.8	603.7	2733.7	3297.6	-496.9
1	2953.8	608.0	2469.4	3258.1	-688.9
3	3447.7	647.1	2785.7	3351.1	-1024.6
4	3444.0	756.5	2700.5	3461.3	-479.5

Principal components analyses of the best subsets of variables are presented in Table 85 PC1 accounts for most of the total variation for all kinds of variables: 0.946 for untransformed head-size variables, 0.962 for log-transformed head-size variables, and 0.632 for ratio variables. This means that an overall cranium size seems to be the major source of variation among animals from different areas of origin, which is similar to the pattern of geographic variation described by Johnsgard (1959) for North American wolves. However, this may be related to direct environmental influences.

Figure 21 shows the plots of wild animals' areas of origin against values for the two principal components. It is possible to see that individuals from *Duraflora* are clustered apart, which is compatible to the geographic location of this study site. However, the other sites are not well individualized by the plots. Log-transformation did not significantly improve interpretation of the principal components analysis. Ratio variables showed an unclear pattern of distribution of subpopulations.

Table 78 Linear discriminant analysis Response: area of origin Predictor: all ratio variables Groups: study sites (1 *Volta Grande* 2 *Porto de Areia* 3 *Fantinal* 4 *Charqueada* and 5 *Duraflora*) Sample size: 29 animals

a) Summary of classification with cross-validation

Group	2	5	1	3	4
2	6	2	0	1	0
5	3	6	2	1	0
1	0	3	0	0	1
3	0	0	0	1	1
4	0	1	0	0	1
Total N	9	12	2	3	3
N Correct	6	6	0	1	1
Proportion	0.667	0.500	0.000	0.333	0.333

N = 29 N Correct = 14 Proportion Correct = 0.483

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS
2	−3921.7	210.2	7392.9	2646.3	4947.3	1755.2	702.6	−4932.7	−763.3
5	3798.0	254.0	7252.4	2634.4	4840.9	1700.7	703.3	−4748.4	−697.1
1	3881.2	−428.7	7527.8	2714.2	4644.2	1692.4	815.7	−4662.8	−653.1
3	3663.5	56.3	6958.2	2486.4	4878.4	1695.1	−622.2	−4797.2	−720.9
4	3837.0	−294.9	7232.2	2626.7	4702.7	1735.3	−678.2	−4659.9	−428.2

	RLSS	RWM
2	6848.1	798.6
5	6456.6	−712.8
1	6132.1	588.4
3	6666.8	875.1
4	6078.5	591.7

Table 79 Principal components analysis Eigenanalysis of the covariance matrix of all log transformed head size variables. Sample size: 29 animals Only first six principal components are presented.

Eigenvalue	0.099773	0.001720	0.000970	0.000688	0.000532	0.000418
Proportion	0.951	0.016	0.009	0.007	0.005	0.004
Cumulative	0.951	0.967	0.975	0.982	0.987	0.991
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0.261	0.128	0.804	-0.041	0.046	0.188
CW	-0.246	-0.085	-0.230	0.026	0.099	0.086
SL	-0.336	0.257	0.151	-0.173	-0.175	0.162
SW	-0.304	-0.034	-0.130	0.103	-0.151	0.312
OL	-0.186	0.094	-0.324	-0.444	0.534	-0.139
OW	-0.213	0.351	0.241	0.185	0.355	-0.029
IOW	-0.321	-0.821	0.346	0.029	0.036	-0.090
LCR	-0.204	-0.023	0.340	-0.215	0.458	-0.852
WN	-0.255	-0.114	-0.493	-0.221	-0.186	-0.491
PXS	-0.305	0.285	0.816	0.607	-0.020	-0.574
ML	-0.291	0.040	-0.141	-0.027	-0.142	0.248
LMS	-0.302	0.209	0.338	-0.372	-0.496	-0.122
WSR	-0.284	-0.057	-0.272	0.349	0.185	0.396

Table 80 Principal components analysis. Eigenanalysis of the covariance matrix of nli ratio variables. Sample size 29 animals. Only first six principal components are presented

Eigenvalue	0.0049066	0.0031213	0.0019718	0.0005788	0.0003577	0.0001166
Proportion	0.432	0.275	0.174	0.051	0.032	0.010
Cumulative	0.432	0.707	0.881	0.932	0.963	0.974
Variable	PC1	PC2	PC3	PC4	PC5	PC6
RCW	-0.022	-0.251	0.464	0.302	-0.254	0.209
RLST	-0.338	0.036	0.340	0.269	0.129	-0.633
RWST	0.686	-0.594	-0.076	-0.030	0.238	-0.285
ROL	0.216	0.173	0.007	0.182	-0.144	0.526
ROW	-0.502	-0.454	-0.641	0.209	-0.258	0.113
RWI	-0.299	-0.555	0.397	-0.456	0.332	0.226
RWN	-0.075	-0.027	0.383	0.215	-0.475	0.292
RPXS	-0.070	-0.061	0.064	0.206	-0.068	-0.190
RLSS	-0.051	0.034	-0.010	0.048	0.095	0.083
RWM	0.110	-0.183	0.003	0.678	0.658	0.081

Table 81 Best subsets of morphometric variables for differences among subpopulations

Variables	Best subsets	P value	r^2	N
Head-size	SW OW IOW WSR	0.000	0.645	29
Log-transformed head-size	SW OW LCR WSR	0.000	0.627	29
Ratios	RCW RLST ROW RLLSS	0.000	0.535	29

Minitab procedure: Stat → Regression → Best Subsets

Table 82 Linear discriminant analysis. Response: area of origin. Predictor: best subset of head-size variables. Groups: study sites (1 *Volta Grande*, 2 *Porto de Areia*, 3 *Pantanal*, 4 *Charqueada*, and 5 *Dureflora*). Sample size: 29 animals

a) Summary of classification with cross validation

Group	2	5	1	3	4
2	6	1	0	1	0
5	1	10	0	0	0
1	0	1	2	0	0
3	1	0	0	1	0
4	1	0	0	1	3
Total N	9	12	2	3	3
N Correct	6	10	2	1	3
Proportion	0.667	0.833	1.000	0.333	1.000

N = 29 N Correct = 22 Proportion Correct = 0.759

b) Linear discriminant function for group

	Constant	SW	OW	IOW	WSR
2	-127.99	-4.52	32.29	21.99	2.79
5	-79.66	-4.75	25.07	18.22	-1.19
1	-102.29	-2.83	26.96	12.37	2.78
3	-161.94	5.85	35.13	38.77	-2.98
4	-152.99	-7.19	33.60	27.42	1.12

Table 83 Linear discriminant analysis Response: area of origin Predictor: best subset of log transformed head-size variables Groups: study-sites (1 *Volta Grande* 2 *Porto de Areia* 3 *Pantanal* 4 *Charqueada* and 5 *Duraflora*) Sample size: 29 animals

a) Summary of classification with cross-validation

Group	2	5	1	3	4
2	6	1	0	0	1
5	0	10	0	0	0
1	0	0	1	0	0
3	1	0	0	2	0
4	2	1	1	1	2
Total N	9	12	2	3	3
N Correct	6	10	1	2	2
Proportion	0.667	0.833	0.500	0.667	0.667

N = 29 N Correct = 21 Proportion Correct = 0.724

b) Linear discriminant function for group

	Constant	SW	OW	LCR	WSR
2	-645.0	746.1	38.1	1883.3	-41.0
5	578.4	-834.2	1105.5	1819.1	147.9
1	567.5	-659.9	81.6	1542.6	60.3
3	-723.5	752.0	-9.8	2046.2	-88.0
4	-567.4	-829.1	53.3	1771.2	129.*

Table 84 Linear discriminant analysis Response: area of origin Predictor: best subset ratio variables Groups: study-sites (1 *Volta Grande* 2 *Porto de Areia*, 3 *Pantanal*, 4 *Charqueada*, and 5 *Duraflora*) Sample size: 29 animals

a) Summary of classification with cross-validation

Group	2	5	1	3	4
2	7	0	0	1	0
5	1	9	0	1	1
1	1	1	1	0	0
3	0	2	1	1	0
4	0	0	0	0	2
Total N	9	12	2	3	3
N Correct	7	9	1	1	2
Proportion	0.778	0.750	0.500	0.333	0.667

N = 29 N Correct = 20 Proportion Correct = 0.690

b) Linear discriminant functions for group

	Constant	RCW	RLST	ROW	RLSS
2	799.7	1317.3	-812.1	568.4	2772.6
5	-751.3	1367.9	-89.2	534.2	2599.7
1	-775.7	1334.3	34.3	539.7	2494.7
3	-805.5	1404.7	-136.5	542.9	2607.6
4	-851.1	1441.8	-55.3	606.9	2514.1

It is interesting to compare Figure 21 with Figure 8 in which the estimated age of wild animals presented a surprising result It is possible that age – not area of origin – is the major source of variation between wild animals captured Sexual dimorphism is not as clear in wild as it is in captive animals, possibly because the wild sample is young- and male-biased In addition other environmental factors, such as food availability may also have influenced the results above

Table 05 Principal components analyses for the best subsets of variables for differences among subpopulations

a) Eigenanalysis of the correlation matrix of best subset of head-size variables

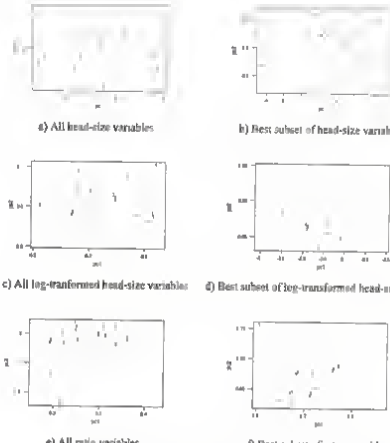
Eigenvalue	3 7857	0 1401	0 0620	0 0114
Proportion	0.946	0 035	0 016	0 003
Cumulative	0.946	0.981	0 997	1 000
Variable	PC1	PC2	PC3	PC4
SW	-0 510	-0.060	0.355	0 780
OW	-0 489	0 706	-0.369	-0 083
IOW	-0 494	-0.606	-0.616	-0 095
WSR	-0.507	-0.099	0 599	-0.612

b) Eigenanalysis of the covariance matrix of best subset of head-size variables

Eigenvalue	0 026144	0 000646	0 000269	0 000116
Proportion	0 962	0.024	0.010	0 004
Cumulative	0 962	0.986	0.996	1 000
Variable	PC1	PC2	PC3	PC4
SW	-0 592	0.368	0 014	-0 717
OW	-0 422	-0 690	0 570	0 002
LCR	-0 400	-0 426	-0 806	0 096
WSR	-0.558	0.443	0 124	0 691

c) Eigenanalysis of the covariance matrix of best subset of ratio variables

Eigenvalue	0 0028213	0 0011533	0 0004377	0 0000500
Proportion	0 632	0 258	0 098	0 011
Cumulative	0 632	0 891	0 989	1 000
Variable	PC1	PC2	PC3	PC4
RCW	-0.021	0 664	-0 734	-0 142
RLST	0 198	0 735	0.630	0 154
ROW	0 979	-0 136	-0 151	0 093
RLSS	0.037	0.019	0.205	-0 978



a) All head-size variables b) Best subset of head-size variables

c) All log-tranformed head-size variables d) Best subset of log-transformed head-size variables

e) All ratio variables f) Best subset of ratio variables

Figure 21 Morphometric differences among subpopulations. Plots of wild animals' areas of origin against values for the two principal components (1 *Volta Grande*, 2 *Porto de Areia*, 3 *Fantasia*, 4 *Charqueada*, and 5 *Dureflora*).

4.4.2 Differences between Wild and Captive Animals

Behavioral changes are usually observed in wild animals maintained in captivity. In some cases, in order to increase efficiency of reintroduction programs, these animals have to be "trained" before released (Box 1991). Although morphological alterations caused by captive environment are frequently assumed as usual, they have been rarely quantified or even described in literature.

Meers (1996) reports morphometric differences between wild and captive American alligators. According to him, the morphological changes caused by the captive environment could be deleterious for released animals. However, Elsey *et al* (1992) reports that farm-released juveniles presented better performances than wild animals both in terms of growth rates and general body conditions.

Crocodilians are assumed to be opportunistic predators with an insignificant role of parents on the guidance of hatchlings and young about how to catch food, although in some circumstances, they may present elaborate methods of prey capture (Lang 1987). This apparently "intuitive" capacity seems to explain the results reported by Elsey *et al* (1992). However, if on one hand, captivity seems not to affect crocodilians feeding behavior plasticity, on the other hand, it may affect their reproductive capacity due to diet deficiencies or stress (Lance 1987).

Feral pigs in Brazilian Pantanal and Southeast United States are easily recognized by local people because of their unique long-snouted aspect, which gives them the name *alongados* in Brazilian Portuguese. This morphological characteristic, possibly related with feeding behavior, is more likely related to a high phenotypic plasticity than to genetic variation since the animals acquire it just in the feral condition. However, the most interesting aspect of this pattern is that it permits a prompt identification of this category of individuals, which is the object of the present study concerning wild and captive young JSC. For this purpose, captive individuals of the same range of body length (SVL) were compared with wild animals in terms of the morphometric variables showed in Figure 1 and described in Table 1 (Section 3.1). The questions and statistical methods showed in Figure 2 (Section 3.3) are presented and discussed below.

There is a significant difference between wild and captive animals in terms of their cranial morphometry (P-values < 0.000 for Wilk's, Lawley-Hotelling, and Pillai's Tests of MANOVA) for the whole set of untransformed and log-transformed head-size variables, and ratio variables. The covariance between animals body-length (SVL) and environment is presented by head-size and ratio variables in Table 8.6. Two of thirteen head-size variables (WN, LMS), and five of eleven ratio-variables (RCW, RWST, RWN, RLSS, RWM) expressed significant differences between wild and captive animals as covariates of SVL (P-value < 0.100).

Significant differences in ANCOVA mean that animals from different environment present significant differences in the allometric relations between SVL and the morphometric variable in question. The biological meaning for this is a significant difference in cranial shape between wild and captive animals.

Captive animals presented higher average values for all significant variables described in Table 86 below (P values < 0 01 in the analyses of variance - ANOVA) This means that captive animals present relativaly broader snout and cranium, longer mandibular symphysis broader mandible and wider external nares This is possibly not related to biomechanical stress and strain caused by food, as described by Bernaye (1986) for insects, since food in captivity consists basically of ground meat Instead, it is more likely caused by the hard pavement of captive enclosures, whereupon the captive animals remain for most of the time The head of a caiman is massive enough to cause a considerable pressure on its own basis resulting on the bone remodeling described above

Table 86 Analysis of covariance Environment (wild and captive) as covariate of SVL.

Variable	SVL	Environment	Variable	SVL	Environment
DCL	0 000	0.251	RCW	0 000	0 000
CW	0 000	0.232	RLST	0 000	0.217
SL	0 000	0.205	RWST	0 000	0 001
SW	0 000	0 108	ROL	0 001	0 402
OL	0 000	0 954	ROW	0 000	0 711
OW	0 000	0.392	RWI	0 000	0 535
IOW	0 000	0.530	RWN	0 000	0 096
LCR	0 000	0 132	RPXS	0 000	0 879
WN	0 000	0 086	RLSS	0 368	0 006
PXS	0 000	0 652	RWM	0 047	0 000
LMS	0 000	0 002			
WSR	0 000	0 757			
LM	0.000	0.428			

Minitab procedure. Stat → ANOVA → General Linear Model
Response (dependent variables) morphometric variables
Model (independent variable) *SVL*
Covariates *Environment* (wild or captivity) for wild and captive non-hatchlings

The results above are somewhat similar to those described by Meers (1996) for captive American alligators Meers found that captive animals present relatively shorter and broader snout. In the present study captive BSC presented indeed a broader snout than wild individuals whereas no difference was found in terms of the relative snout-length between wild and captive animals As mentioned by Meers, distinct biomechanical pressures possibly leads to distinct results on the sculpting of the skull of wild and captive animals Orthodontists use similar concepts in remodelling humans' dentition (Graber 1972)

Linear discriminant analysis with cross-validation for the whole set of both untransformed (Table 87) and log transformed head size variables (Table 88), and ratio variables

(Table 89) showed relatively high proportions of correct classification. Log-transformation did not significantly improve results. Ratio variables presented similar results to untransformed head size variables. This is unusual in relation to the studies of age, sexual dimorphism and clutch discrimination, but can be explained by the analysis of covariance presented above (Table 86).

Table 87. Linear discriminant analysis. Response environment. Predictor: all head-size variables. Sample size, 103 animals. Groups: wild and captive animals.

a) Summary of classification with cross validation

Group	Captive	Wild
Captive	64	4
Wild	18	25
Total N	74	29
N Correct	64	25
Proportion	0.865	0.862

N = 103 N Correct = 89 Proportion Correct = 0.864

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
Captive	-111.90	2.80	-6.17	-6.68	1.32	7.84	7.40	1.93	7.60	8.58
Wild	-122.03	3.26	-6.93	-6.89	1.18	7.47	7.66	2.75	9.59	6.04

	PXS	ML	LMS	WSR
Captive	-0.18	0.06	-0.91	0.17
Wild	-0.12	0.21	1.17	0.18

Table 88. Linear discriminant analysis. Response environment. Predictor: all log-transformed head-size variables. Sample size: 103 animals. Groups: wild and captive animals.

a) Summary of classification with cross-validation

Group	Captive	Wild
Captive	66	4
Wild	8	25
Total N	74	29
N Correct	66	25
Proportion	0.892	0.862

N = 103 N Correct = 91 Proportion Correct = 0.883

b) Linear discriminant function for group

	Constant	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN
Captive	2078.5	4739.4	66.7	2152.9	526.7	144.2	296.5	58.6	232.6	548.8
Wild	2166.5	4839.1	39.2	-2174.4	556.2	132.6	308.3	-41.5	323.4	-608.0

	PXS	ML	LMS	WSR
Captive	95.5	638.1	-726.0	-719.6
Wild	-92.5	690.4	-745.0	-711.6

Table 89 Linear discriminant analysis Response environment Predictor all ratio variables Sample size 103 animals Groups wild and captive animals

a) Summary of classification with cross-validation

Group	Captive	Wild
Captive	64	4
Wild	10	25
Total N	74	29
N Correct	64	25
Proportion	0.865	0.862

N = 103 N Correct = 89 Proportion Correct = 0.864

b) Linear discriminant function for group

	Constant	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS
Captive	-2302.4	260.5	4626.2	1141.8	3608.3	721.1	223.1	1781.8	140.7
Wild	-2254.8	-280.7	4645.3	1129.4	3623.3	728.8	242.5	1891.9	147.3

	RLSS	RWM
Captive	897.7	125.5
Wild	834.3	105.5

PCA of untransformed (Table 90) and log-transformed head-size variables (Table 91) presented similar results. PC1 accounted for most of the total variation in both cases (0.892 for the former and 0.896 for the later). Log-transformation was responsible for a significant concentration of variation on the first remaining principal component (PC2). It responded for twice as much as the variation contained in PC2 of untransformed variables (0.042 against 0.027). In this case, therefore, log-transformation improved sensibility of the model to perceive shape variation between groups.

PC1 coefficients of untransformed variables are similar in magnitude and sign, varying from -0.247 for IOW to -0.291 for CW. PC1 coefficients of log transformed variables are also similar in sign, but presented a larger range, varying from -0.158 for OW to -0.362 for IOW. This means that most of the cranial morphometric variation between individuals is the overall size of skull.

PC2 of untransformed variables shows a clear contrast between OW (-0.654) and IOW (0.742), whereas IOW alone responds for most of the variation of PC2 for log-transformed variables (0.919). These patterns are similar to the results of principal components analyses of the whole sets of variables for captive and wild animals separated (see Tables 8.9 and 27). They are also similar to the PCA of the best subsets of variables for sexual dimorphism in captive animals (see Figure 38). However, they slightly vary from the patterns showed by the PCA for

the best subsets of variables for age determination in captive animals. A possible reason for this is that gender- and age-effect are not isolated from environmental effect in the present study although gender effect seems to be stronger in this case, since all animals are young.

Table 90. Principal components analysis. Eigenanalysis of the correlation matrix of all head-size variables. Sample size: 29 wild animals. Only six first principal components are presented.

Eigenvalue	11.592	0.346	0.318	0.200	0.139	0.116
Proportion	0.892	0.027	0.024	0.015	0.011	0.009
Cumulative	0.892	0.918	0.943	0.958	0.969	0.978
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0.289	-0.042	-0.077	0.159	-0.178	0.031
CW	-0.291	0.022	-0.154	-0.002	0.091	-0.137
SL	-0.289	0.009	0.011	0.029	-0.105	0.045
SW	-0.268	0.028	-0.183	0.045	0.083	-0.217
OL	-0.269	-0.007	-0.497	0.316	0.389	0.510
OW	-0.250	-0.654	0.563	0.164	0.367	-0.068
IOW	-0.247	0.742	0.522	0.147	0.231	0.073
LCR	-0.277	-0.048	0.093	0.510	0.406	0.118
WN	-0.279	0.064	-0.089	-0.412	0.444	-0.220
PXS	-0.273	-0.062	0.211	-0.518	-0.298	0.538
ML	-0.281	0.056	-0.028	0.010	-0.347	-0.490
LMS	-0.279	-0.077	-0.062	-0.353	-0.169	0.107
WSR	-0.287	-0.016	-0.184	0.027	-0.019	-0.239

Table 91. Principal components analysis. Eigenanalysis of the covariance matrix of all log-transformed head-size variables. Sample size: 29 wild animals. Only six first principal components are presented.

Eigenvalue	0.004222	0.003985	0.001683	0.001071	0.000809	0.000590
Proportion	0.896	0.042	0.018	0.011	0.009	0.006
Cumulative	0.896	0.939	0.957	0.968	0.977	0.983
Variable	PC1	PC2	PC3	PC4	PC5	PC6
DCL	-0.248	-0.086	0.183	0.215	0.120	-0.025
CW	-0.287	-0.104	0.204	-0.064	-0.089	0.896
SL	-0.322	-0.061	0.039	0.171	0.054	-0.184
SW	-0.299	-0.105	0.264	-0.080	-0.056	0.052
OL	-0.185	-0.116	0.323	-0.031	0.119	0.023
OW	-0.158	-0.154	-0.342	0.553	-0.660	0.026
IOW	-0.362	0.919	-0.049	-0.008	-0.072	-0.020
LCR	-0.192	0.003	0.044	0.441	0.164	-0.075
WN	-0.282	-0.103	0.046	-0.548	-0.541	0.107
PXS	-0.313	-0.143	-0.759	-0.235	0.329	0.276
ML	-0.301	-0.968	0.085	0.171	0.280	0.324
LMS	-0.300	-0.164	-0.120	-0.166	0.068	-0.830
WSR	-0.278	-0.140	0.226	-0.012	0.027	0.256

Table 92 Principal components analysis Eigenanalysis of the covariance matrix of all ratio variables Sample size 29 wild animals Only six first principal components are presented

Eigenvalue	0.0061737	0.0044572	0.0032479	0.0013534	0.0007568	0.0002795
Proportion	0.368	0.266	0.194	0.081	0.045	0.017
Cumulative	0.368	0.634	0.828	0.909	0.954	0.971
Variable	PC1	PC2	PC3	PC4	PC5	PC6
RCW	0.051	0.202	0.338	0.469	-0.069	-0.242
RLST	0.228	0.212	0.060	-0.371	-0.047	-0.216
RWST	-0.708	-0.081	0.595	0.134	-0.209	0.029
ROL	-0.158	0.018	-0.104	-0.037	0.031	0.164
ROW	0.341	0.867	0.312	-0.117	-0.027	-0.084
RWI	0.481	0.348	0.601	0.469	0.286	0.045
RWN	0.121	0.177	0.195	-0.515	-0.154	-0.024
RPXS	0.187	0.014	0.105	0.232	-0.187	0.912
RLSS	-0.084	-0.013	0.007	-0.117	0.183	0.159
RWM	-0.216	-0.056	0.097	0.238	0.912	0.022

PCA of ratio variables shows a more complex pattern with PC1 and PC2 accounting for respectively 0.368 and 0.266 of the total variation RWST (-0.708) is the major source of variation in PC1 whereas ROW (-0.867) is the major source of variation in PC2 Both ratios are size dependent (see Table 21) Coefficients of PC1 and PC2 vary both in sign and magnitude. There is a clear contrast in PC1 between RWST and the association between ROW (0.341) and RWI (0.481) This possibly represents a straightening of the snout (RWST with negative sign) in relation to the eyes region of the skull (ROW and RWI with positive sign) This is compatible with the results of ANCOVA (Table 86) and subsequent ANOVA, in which wild animals present a relatively narrower snout.

Table 93 presents the best subsets of variables for the study of morphometric differences between wild and captive animals Log transformation did not significantly affect the model. Both untransformed and log transformed data presented the same best subsets of variables.. equally divided into width- and length-variables The best subset of ratio variables, however contained only width-variables, which is compatible to the ANCOVA results (Table 86), discussed above.

Table 93 Best subsets of morphometric variables for environment (wild and captivity)

Variables	Best subsets	P value	r^2	N
Head-size	CW LCR, WN ML	0.000	0.590	103
Log transformed head-size	CW LCR, WN ML	0.000	0.604	103
Ratios	RWST RWI RWN RWM	0.000	0.532	103

Minitab procedure Stat → Regression → Best Subsets

There is still a significant difference on the cranial morphometry of wild and captive animals even after a reduction in the number of variables (P values < 0 000 for Wilk s Lawley Hetelling, and Pillai s Tests of MANOVA for all best subsets of variables) Linear discriminant analyses with cross-validation for the best subset of both untransformed (Table 94) and log-transformed head-size variables (Table 95) and ratio variables (Table 96) presented even higher proportions of correct classification Log transformation did not significantly improve results Ratio variables presented intermediate results (0 893) between untransformed (0 903) and log-transformed head-size variables (0 883). This is unusually high for ratio variables, as seen in former sections, but can be explained by the results of the analysis of covariance (Table 86)

Table 94 Linear discriminant analysis Response environment Predictor best subset of head size variables Sample size 103 animals Groups wild and captive animals.

a) Summary of classification with cross-validation

Group	Captive	Wild
Captive	65	3
Wild	9	26
Total N	74	29
N Correct	65	26
Proportion	0 878	0 897

N = 103 N Correct = 91 Proportion Correct = 0 883

b) Linear discriminant function for group

	Constant	CW	LCR	WN	ML
Captive	-41 780	-1 847	8 711	3 077	-8.334
Wild	51 967	2.420	10 887	0.589	8 153

Table 95 Linear discriminant analysis Response environment Predictor best subset of log-transformed headsize variables Sample size 103 animals Groups wild and captive animals

a) Summary of classification with cross-validation

Group	Captive	Wild
Captive	66	2
Wild	8	27
Total N	74	29
N Correct	66	27
Proportion	0 892	0 931

N = 103 N Correct = 93 Proportion Correct = 0 903

b) Linear discriminant function for group

	Constant	CW	LCR	WN	ML
Captive	-619 8	669 9	338 3	-1204.2	504.3
Wild	-670.0	525 1	446 8	1266 9	562 4

Table 96 Linear discriminant analysis Response environment Predictor Best subset of ratio variables Sample size 103 animals Groups wild and captive animals

a) Summary of classification with cross validation

Group	Captive	Wild
Captive	67	4
Wild	7	25
Total N	74	29
N Correct	67	25
Proportion	0 905	0 862

N = 103 N Correct = 92 Proportion Correct = 0 893

b) Linear discriminant function for group

	Constant	RWST	RWI	RWN	RWM
Captive	-482 58	330 72	45 91	975 24	576 28
Wild	-425 05	314 50	64 85	861 78	545 09

PCA of the best subsets of untransformed (Table 97a) and log-transformed head-size variables (Table 97b) present similar results. PC1 accounts for most of the variation in both cases (0 933 for the former and 0 945 for the later) With the reduction in the number of variables log transformation no longer is responsible for a significant concentration of variation on PC2 (0 034 against 0 040 in PC2 for untransformed variables)

PC2 of both untransformed and log-transformed variables show a clear contrast between LCR and WN ML also contributes significantly for the variation after log-transformation of data In these contrasts the rearrangement in the eye region of the head in relation to its width -- possibly more associated with ontogenetic processes and sexual dimorphism is not present. This may be a good indication that these two processes were significantly isolated from the analysis of the environmental effect, after reducing the number of variables A relationship between the width of snout and the length of head (here best represented by WN and LCR) seems to be the major source of variation between wild and captive animals

PCA of the best subset of ratio variables (Table 97c) presented as usual a less pronounced concentration of variation in PC1 and a significant amount of variation in PC2 and the remaining principal components (0 556 0 298 and 0 146 respectively) The major source of variation in PC1 is RWST (0 792) which seems to reemphasize the patterns described above. However the relative interorbital width (RWI) also contributes significantly for the total amount of variation contained in PC1 No contrast is perceptible in PC2, but its major source of variation is RWI which is a size-independent non-metric variable (see Table 8) This possibly explains a

shape" component in PC2 and also means that the "size" component in PC1 is primarily due to RWST

Table 97 Differences between wild and captive animals Principal components analyses of best subsets of variables Sample size 103 animals

a) Eigenanalysis of the correlation matrix of the best subset of head-size variables.

Eigenvalue	3 7326	0 1581	0 0820	0 0274
Proportion	0 933	0 040	0 020	0 007
Cumulative	0 933	0 973	0 993	1 000
Variable	PC1	PC2	PC3	PC4
CW	-0 512	0 118	0 157	-0 836
LCR	-0 491	-0 729	0 391	0 271
WN	-0 495	0 670	0 312	0 456
ML	-0 502	-0 068	-0 851	0 137

b) Eigenanalysis of the covariance matrix of the best subset of log-transformed head-size variables

Eigenvalue	0 024769	0 000883	0 0003385	0 0001691
Proportion	0 945	0 034	0 015	0 006
Cumulative	0 945	0 979	0 994	1 000
Variable	PC1	PC2	PC3	PC4
Lcw	-0 532	0 055	-0 225	0 814
Llcr	-0 353	-0 543	-0 663	-0 377
Lwn	-0 528	0 735	-0 083	-0 419
Lml	0 569	-0 403	0 709	-0 143

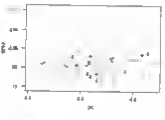
c) Eigenanalysis of the covariance matrix of the best subset of ratio variables

Eigenvalue	0 0053884	0 0028845	0 0007781	0 0005380
Proportion	0 558	0 298	0 080	0 066
Cumulative	0 558	0 854	0 934	1 000
Variable	PC1	PC2	PC3	PC4
RWST	0 792	-0 565	-0 207	0 102
RWL	-0 541	-0 803	0 002	0 249
RWN	-0 134	-0 183	0 416	0 880
RWM	0 247	-0 048	0 885	-0 391

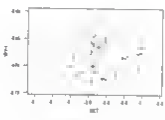
Figure 22 shows the plots of individuals environment against values for the two principal components It is clear that the use of the best subset of variables stressed the variation between wild and captive animals (compare plots b and f respectively with a and e). It is also clear that this variation is basically due to shape differences between wild and captive animals (see in plots b and f that PC2 axis is the major source of variation) Thus means that wild and captive animals with similar skull size present a significant difference in the skull shape

a) All head-size variables

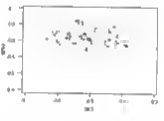
b) Best subset of head-size variables



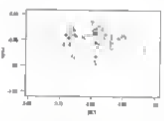
c) All log-transformed head-size variables



d) Best subset of log-transformed head-size variables



e) All ratio variables



f) Best subset of ratio variables

Figure 22 Differences between wild and captive animals. Plots of individuals' environment against values for the two principal components (w wild, c captivity)

CHAPTER 5
SUMMARY AND CONCLUSIONS

Three consecutive questions are tested in the present morphometric study of the broad-snouted caiman (*Caiman latirostris*). Is there a significant morphometric variation caused by *clutch-effect, body size, sex, age, area of origin* and *environment*? Can the group of variables above to which a specific individual belongs be predicted? Lastly, is it possible to reduce the number of variables without significantly loosing efficiency?

Cranial and body morphometric variables were recorded from captive and wild animals. Ratios and log-transformation of data are presented and discussed. MANOVA, linear discriminant analysis with cross-validation, PCA, and best subset regressions are used in order to answer the questions above. Exploratory studies of relative growth and allometry of reproduction are used to develop models of age estimation, sexual dimorphism, and clutch discrimination. Ontogenetic changes show major variation in upper jaw/cranium which may be associated with animal-animal signaling, social structure, in the sense that these are the regions of the body usually exposed above surface of the water. The patterns of cranial relative growth found suggests a possible relationship between social behavior and ontogenetic changes.

Except for sexual dimorphism studies, and also for the specific case of body mass (BM) in growth curves and allometric relations, log-transformation did not significantly improve data analysis in the present study. Ratio variables, in their turn, were consistently less efficient in detecting differences between groups than head-size variables and consistently presented unclear patterns of variation distribution in principal components analysis. The "shape" information contained in ratios may be substituted by the better quantification of shape and size variation of principal components analyses of direct measurements. Table 9B presents the best subsets of cranial morphometric variables for age estimation, sexual dimorphism, clutch discrimination, matrilineal lineage (female-family) effect, geographic variation (effect of area of origin), and environmental effect (differences between wild and captive animals).

Multivariate morphometric models are consistently more efficient than univariate growth curves to determine age of animals. Snout-vent length (SVL) or body mass (BM) alone in captive BSC is less efficient than some single head measurements, like dorsal cranial length (DCL).

snout length (SL) or cranial width (CW). Cranial morphometry seems to be more pronouncedly age-dependent and less dependent on growth rates than body length (SVL) or body mass (BM). The age estimation of wild animals, based on cranial morphometry of captive animals, may be viable. Field studies are urged to test this method with wild animals of known age.

Table 98. Summary of best subsets of variables

	Category	Data	Morphometric variables
Age estimation	Captive	Head-size	CW, SL, SW, PXS
		Log head size*	CW, IOW, LCR, PXS
		Ratio	RCW, RLST, RWST, RWI
Sexual dimorphism	Wild	Head-size	DCL, CW, SL, OL, OW, IOW, LCR, WN, PXS, LMS, WSR
	Captive	Head-size	CW, SW, OL, OW, IOW, LCR, WN, PXS, ML, LMS, WSR, LM
		Log-head size*	SW, OL, OW, ML, WSR, LM
		Ratio	RLST, RWST, ROW, RWI, RLSS, RWM, RLLMR
Clutch effect	Eggs	Measurements	egg mass, egg width
		Log-measur *	egg mass, egg width
	Hatchlings	Head size	OL, ML, WSR, LM
		Log head size*	OL, ML, WSR, LM
		Ratio	ROL, RWI, RWM, RLLMR
Female-family effect	Eggs	Measurements	egg mass, egg width
		Log measur *	egg mass, egg width
	Hatchlings	Head size	CW, SL, OL, WSR
		Log-head size*	CW, SL, OL, WSR
		Ratio	RLST, ROL, RWM, RLLMR
Geographic variation	Wild	Head-size	SW, OW, IOW, WSR
		Log-head size*	SW, OW, LCR, WSR
		Ratio	RCW, RLST, ROW, RLSS
Environmental effect	Wild & Captive	Head size	CW, LCR, WN, ML
		Log head size*	CW, LCR, WN, ML
		Ratio	RWST, RWI, RWN, RWM

* Log transformed head-size variables

Sexual dimorphism in cranial morphometry of BSC can be detected even in young individuals. However, it is frequently impossible to isolate other sources of variation, such as age, body size, and environment, from gender. Sexual dimorphism was detected in the allometric growth of BW, OL, OW, RCW, RLST, ROL, ROW, and RWN. With the exception of BW, all these morphometric variables are located in the cranium, and none in the mandible. This is compatible with normal crocodilians social displays, in which the mandible is usually kept under the water.

BSC has a positive correlation between female body size (BM and SVL) and egg size (mass, width and length), hatchlings body size (BM and SVL) and clutch mass. There is a significant negative correlation between female body size (BM and SVL) and the relative clutch mass (clutch mass / female BM). The investment in clutch mass drops down approximately 50%, when female BM increases from 20 to 40 kg. However, no significant correlation was found between female body size (BM and SVL) and clutch size.

There is a consistent clutch effect on eggs shape and size, and hatchlings cranial morphometry. Based on two or three egg measurements (mass, width, and length, in decreasing order of importance) it is possible to discriminate eggs from different clutches with consistently high rates (above 70%), even in homogeneous groups of related reproductive females. Similarly it is possible to discriminate hatchlings from different clutches with even higher rates (above 88% with the whole set and approximately 80% with reduced set of four "best" cranial morphometric variables).

Compared to clutch effect, matrilineal lineages have even more consistent effect in the shape and size of eggs, and in the cranial morphometry of hatchlings. Even in a small group of related reproductive females, it was possible to discriminate clutches (eggs and hatchlings) from different female-families with virtually 100% chance (approximately 95% for eggs, and above for hatchlings, with best subset of four cranial morphometric variables). Clutch discrimination based on clutch effect and female-family effect (matrilineal lineage) can be used to establish parentage amongst individuals in small wild populations and captive breeding programs. For its low cost, these methods can be used to complement more expensive biochemical tests of paternity.

There is a significant cranial morphometric variation among animals from different geographic areas of origin. The present study sites are not excessively far from each other, and are interconnected by watercourses. The perceptible morphometric differences between these subpopulations may be related to some level of reproductive isolation, which may related to human induced habitat fragmentation. Captive animals present relatively broader snout and cranium, longer mandibular symphysis, broader mandible, and wider external nares than wild individuals, possibly due to bone remodeling caused by the hard pavement of captive enclosures rather than differences in feeding habits.

Although geometric morphometrics led to significant advances on the graphic representation of living organisms form, traditional multivariate morphometrics can still be extremely useful for discriminatory studies. Not only interspecific variation -- the traditional

field of morphometricians -- but also intraspecific morphometric variation can be successfully studied by multivariate morphometrics. In the present study, traditional multivariate morphometric analyses are used to evaluate the effect of aging, ontogenetic growth, sexual dimorphism, clutch effect, matrilineal lineage, geographic variation, and environment in BSC morphometry.

The morphometric models developed in the present study might represent an inexpensive but effective set of methods for the metapopulation modeling and conservation of the broad-snouted caiman in São Paulo, Brazil. The conservation of local populations in São Paulo may be essential to prevent geographic isolation between northern and southern populations of the species considering its overall geographic distribution.

The assessment of individual's sex and age might lead us to the establishment of the population's sex ratio and age structure. The establishment of parentage among individuals based on clutch discrimination might lead us to the assessment of mating system and dispersal pattern. Consequently, it might result in a better understanding of the colonization-local extinction recolonization process of anthropogenic and remaining habitats of the species in São Paulo on a metapopulation context.

Understanding how an endangered species respond to deep human pressure may help us to predict other species responses in similar situations. In a certain sense, what is happening in São Paulo today, both in terms of the human impact on wildlife species and habitats and their response to this impact, is likely to happen in the future in other regions of Brazil. In other words, understanding how some wild species "learn" to live with us might help to learn how to live with them.

Appendix A
Descriptive Statistics of Morphometric Variables

Descriptive statistics of morphometric variables, average, standard deviation R-coefficient and P-value of Ryan-Joiner test of Normality (Ryan and Joiner, 1976) R-coefficient is similar to Shapiro-Wilk test W (Shapiro and Wilk 1965) and the Shapiro-Francia approximation W (Shapiro and Francia 1972) N sample size (males females, unknown)

I. Wild animals

Variable	average	StDev	R	P-value
BM kg	0 684	0 569	0 9433	< 0 0100
SVL cm	30 131	6 776	0 9663	0 0761
TTL cm	59 683	12 807	0 9729	0 0340
BW	103 341	30 889	0 9370	< 0 0100
DCL	70 421	13 844	0 9708	> 0 1000
CW	45 441	10 163	0 9635	0 0688
SL	32 241	7 905	0 9733	> 0 1000
SW	36 307	8 133	0 9718	> 0 1000
OL	19 234	4 282	0 9776	> 0 1000
OW	12 176	1 863	0 9839	> 0 1000
IOW	5 717	1 417	0 9850	> 0 1000
LCR	20 139	3 125	0 9824	> 0 1000
WN	9 697	1 725	0 9730	> 0 1000
PXS	13 763	3 146	0 9745	> 0 1000
ML	83 231	18 261	0 9681	0 0876
LMS	11 416	2 579	0 9669	0 0787
WSR	42 328	9 237	0 9681	0 0873
LM	------	------	------	------
RCW	0 643	0 027	0 9394	0 0408
RLST	0 434	0 030	0 9762	> 0 1000
RWST	1 334	0 059	0 9818	> 0 1000
ROL	0 276	0 021	0 9653	0 0829
ROW	0 633	0 053	0 9678	0 0849
RWI	0 295	0 043	0 9789	> 0 1000
RWN	0 227	0 019	0 9617	0 0468
RPXS	0 194	0 013	0 9823	> 0 1000
RLSS	0 137	0 008	0 9701	> 0 1000
RWM	0 512	0 034	0 9823	> 0 1000
RLMR	------	------	------	------

N=29 (24 5 0)

II. Captive hatchlings

Variable	average	StDev	R	P value
BM g	46 887	6 613	0 9613	< 0 0100
SVL cm	11 628	0 530	0 9908	0 0893
TTL cm	24 378	1 285	0 9933	> 0 1000
BW	------	------	------	------
DCL	33 254	1 185	0 9961	> 0 1000
CW	21 375	0 944	0 9931	> 0 1000
SI	11 070	0 822	0 9929	> 0 1000
SW	14 789	0 759	0 9964	> 0 1000
OL	11 521	0 776	0 9970	> 0 1000
OW	8 055	0 570	0 9866	0 0340
IOW	2 370	0 299	0 9963	0 0317
LCR	12 845	0 567	0 9982	> 0 1000
WN	5 006	0 344	0 9892	0 0482
PXS	5 905	0 344	0 9930	> 0 1000
ML	34 357	1 467	0 9908	0 0887
LMS	3 144	0 315	0 9958	> 0 1000
WSR	19 875	0 951	0 9916	> 0 1000
LM	17 315	0 964	0 9976	> 0 1000
RCW	0 643	0 017	0 9931	0 0695
RLST	0 333	0 010	0 9798	< 0 0100
RWST	1 341	0 060	0 9832	< 0 0100
ROL	0 346	0 018	0 9716	< 0 0100
ROW	0 700	0 034	0 9963	> 0 1000
RWI	0 306	0 034	0 9814	< 0 0100
RWN	0 338	0 014	0 9931	> 0 1000
RPXS	0 176	0 011	0 9912	0 0098
RLSS	0 149	0 009	0 9962	> 0 1000
RWM	0 576	0 029	0 9963	> 0 1000
RLMR	0 498	0 023	0 9963	> 0 1000

N=124 (0 0 124)

III Captive 1-year old animals

Variable	average	StDev	R	P value
BM kg	0 175	0 070	0 9576	> 0 1000
SVL cm	18 383	2 335	0 9717	> 0 1000
TTL cm	37 769	4 209	0 9825	> 0 1000
BW	79 625	19 926	0 9435	0 0589
DCL	47 325	4 611	0 9504	> 0 1000
CW	30 363	3 348	0 9706	> 0 1000
SL	19 213	2 908	0 9854	> 0 1000
SW	23 650	2 854	0 9835	> 0 1000
OL	14 188	0 889	0 9730	> 0 1000
OW	11 006	1 242	0 9679	> 0 1000
IOW	2 944	0 261	0 9908	> 0 1000
LCR	14 081	1 221	0 9812	> 0 1000
WN	6 775	0 737	0 9701	> 0 1000
PXS	9 856	1 613	0 9708	> 0 1000
ML	53 419	5 600	0 9888	> 0 1000
LMS	8 050	0 906	0 9809	> 0 1000
WSR	28 594	3 527	0 9804	> 0 1000
LM	27 556	3 293	0 9528	0 0997
RCW	0 641	0 018	0 9825	> 0 1000
RLST	0 404	0 023	0 9681	> 0 1000
RWST	1 236	0 072	0 9894	> 0 1000
ROL	0 301	0 019	0 9608	> 0 1000
ROW	0 775	0 061	0 9204	0 0180
RWI	0 208	0 016	0 9817	> 0 1000
RWN	0 241	0 017	0 9774	> 0 1000
RPXS	0 208	0 022	0 9899	> 0 1000
RLSS	0 151	0 007	0 9712	> 0 1000
RWM	0 535	0 017	0 9807	> 0 1000
RLLMR	0 516	0 025	0 9647	> 0 1000

N=16 (14 2 0)

IV Captive 2-year old animals

Variable	average	StDev	R	P-value
BM kg	0 730	0 463	0 9590	< 0 0100
SVL cm	30 202	6 264	0 9893	> 0 1000
TTL cm	60 379	12 180	0 9861	> 0 1000
BW	107 032	28 354	0 9944	> 0 1000
DCL	69 686	11 154	0 9944	> 0 1000
CW	47 450	8 613	0 9953	> 0 1000
SL	32 894	8 405	0 9904	> 0 1000
SW	38 084	7 207	0 9932	> 0 1000
OL	19 913	2 440	0 9744	0 0219
OW	11 773	1 163	0 9888	> 0 1000
IOW	5 423	1 412	0 9836	0 0921
LCR	19 165	2 527	0 9961	> 0 1000
WN	9 595	1 734	0 9940	> 0 1000
PXS	13 631	2 829	0 9867	> 0 1000
ML	80 870	15 692	0 9894	> 0 1000
LMS	11 734	2 224	0 9968	> 0 1000
WSR	43 760	7 920	0 9912	> 0 1000
LM	37 421	7 486	0 9912	> 0 1000
RCW	0 879	0 024	0 9888	> 0 1000
RLST	0 458	0 023	0 9962	> 0 1000
RWST	1 130	0 053	0 9759	0 0288
ROL	0 288	0 016	0 9812	0 0614
ROW	0 595	0 048	0 9931	> 0 1000
RWI	0 270	0 052	0 9754	0 0267
RWN	0 254	0 021	0 9957	> 0 1000
RPXS	0 195	0 020	0 9952	> 0 1000
RLSS	0 148	0 010	0 9918	> 0 1000
RWM	0 545	0 028	0 9898	> 0 1000
RLLMR	0 456	0 023	0 9916	> 0 1000

N=62 (2 60 0)

V Captive 3-year old animals

Variable	average	StDev	R	P value
BM kg	1 867	1 069	0 9794	> 0 1000
SVL cm	38 900	7 425	0 9842	> 0 1000
TTL cm	76 192	15 100	0 9837	> 0 1000
BW	152 692	36 436	0 9935	> 0 1000
DCL	87 131	13 619	0 9890	> 0 1000
CW	60 300	10 944	0 9879	> 0 1000
SL	43 785	7 412	0 9847	> 0 1000
SW	48 431	8 645	0 9836	> 0 1000
OL	23 308	2 728	0 9882	> 0 1000
OW	14 431	1 503	0 9697	> 0 1000
IOW	7 400	1 309	0 9547	> 0 1000
LCR	22 917	2 749	0 9753	> 0 1000
WN	12 539	2 117	0 9893	> 0 1000
PXS	19 600	3 937	0 9845	> 0 1000
ML	105 500	18 283	0 9831	> 0 1000
LMS	15 977	3 111	0 9870	> 0 1000
WSR	55 323	10 839	0 9793	> 0 1000
LM	51 215	8 423	0 9934	> 0 1000
RCW	0 690	0 032	0 9552	> 0 1000
RLST	0 502	0 024	0 9745	> 0 1000
RWST	1 107	0 072	0 9450	0 0988
ROL	0 269	0 016	0 9784	> 0 1000
ROW	0 621	0 030	0 9728	> 0 1000
RWI	0 317	0 040	0 9848	> 0 1000
RWN	0 290	0 025	0 9768	> 0 1000
RPXS	0 225	0 014	0 9913	> 0 1000
RLSS	0 152	0 016	0 9109	0 0232
RWM	0 523	0 025	0 8771	> 0 1000
RLLMR	0 487	0 019	0 9556	> 0 1000

N=13 (3 10 01

VI Captive 4-year old animals

Variable	average	StDev	R	P value
BM kg	2 860	2 501	0 9506	> 0 1000
SVL cm	42.300	12.278	0 9959	> 0 1000
TTL cm	84 170	22 066	0 9980	> 0 1000
BW	176 000	60 663	0 9866	> 0 1000
DCL	92 220	32.457	0 9895	> 0 1000
CW	66 340	17 978	0 9997	> 0 1000
SL	47.540	13 770	0 9974	> 0 1000
SW	52 680	12 393	0 9947	> 0 1000
OL	24 280	4 753	0 9933	> 0 1000
OW	15 220	2 157	0 9907	> 0 1000
IOW	8 7600	2.338	0 9775	> 0 1000
LCR	24 400	3 793	0 9728	> 0 1000
WN	13 660	3 172	0 9867	> 0 1000
PXS	20 360	5 975	0 9322	> 0 1000
ML	121 580	36.220	0 9677	> 0 1000
LMS	15 980	3 960	0 9909	> 0 1000
WSR	60 400	15 929	0 9969	> 0 1000
LM	53 520	13 220	0 9941	> 0 1000
RCW	0 715	0 039	0 9361	> 0 1000
RLST	0 510	0 031	0 9345	> 0 1000
RWST	1 123	0 072	0 9526	> 0 1000
ROL	0 266	0 017	0 9725	> 0 1000
ROW	0 632	0 035	0 9710	> 0 1000
RWI	0 357	0 030	0 9801	> 0 1000
RWN	0 304	0 022	0 9684	> 0 1000
RPXS	0 224	0 025	0 9266	> 0 1000
RLSS	0 134	0 017	0 8655	0 0378
RWM	0 505	0 064	0 8960	0 0842
RLLMR	0 449	0 054	0 8452	0 0210

N 5 (0 5 0)

VII. Captive 5 year old animals

Variable	average	StDev	R	P-value
BM kg	7 624	5 145	0 9465	> 0 1000
SVL cm	66 060	13 135	0 9695	> 0 1000
TTL cm	117 740	24 200	0 9556	> 0 1000
BW	268 800	74 632	0 9950	> 0 1000
DCL	129 040	29 016	0 9718	> 0 1000
CW	92 000	20 763	0 9546	> 0 1000
SL	70 360	18 632	0 9513	> 0 1000
SW	77 560	16 573	0 9839	> 0 1000
OL	28 740	4 496	0 9478	> 0 1000
OW	18 160	2 840	0 9548	> 0 1000
IOW	12 768	4 840	0 9694	> 0 1000
LCR	31 940	5 961	0 9777	> 0 1000
WN	18 340	2 981	0 9692	> 0 1000
PXS	29 520	6 232	0 9278	> 0 1000
ML	163 720	32 403	0 9479	> 0 1000
LMS	24 420	4 953	0 9691	> 0 1000
WSR	86 300	17 937	0 9765	> 0 1000
LM	72 800	8 002	0 9998	> 0 1000
RCW	0 709	0 040	0 9437	> 0 1000
RLST	0 539	0 040	0 9456	> 0 1000
RWST	1 116	0 081	0 9102	> 0 1000
ROL	0 224	0 018	0 9718	> 0 1000
ROW	0 634	0 054	0 9634	> 0 1000
RWI	0 439	0 098	0 9802	> 0 1000
RWN	0 312	0 034	0 9638	> 0 1000
RPXS	0 230	0 033	0 9226	> 0 1000
RLSS	0 149	0 007	0 9733	> 0 1000
RWM	0 526	0 024	0 9530	> 0 1000
RLLMR	0 517	0 047	0 9129	> 0 1000

N=5 (2 3 0) For LM and RLLMR N 3 (2 1 0)

VIII. Captive > 5 year old

Variable	average	StDev	R	P-value
BM kg	29 258	12 201	0 9446	0 0434
SVL cm	87 273	12 437	0 9630	> 0 1000
TTL cm	166 701	20 160	0 9543	0 0795
BW	434 211	61 334	0 9826	> 0 1000
DCL	179 074	23 443	0 9323	0 0213
CW	146 021	23 746	0 9114	< 0 0100
SL	105 300	15 262	0 9321	0 0209
SW	112 911	16 039	0 9313	0 0194
OL	38 068	4 222	0 9365	0 0290
OW	24 295	3 584	0 9815	> 0 1000
IOW	19 147	2 267	0 9782	> 0 1000
LCR	41 779	5 280	0 9678	> 0 1000
WN	26 442	3 047	0 9840	> 0 1000
PXS	38 705	8 858	0 9698	> 0 1000
ML	230 353	31 642	0 9291	0 0155
LMS	34 826	5 189	0 9690	> 0 1000
WSR	137 968	21 200	0 9270	0 0118
LM	------	------	------	------
RCW	0 813	0 037	0 9672	> 0 1000
RLST	0 587	0 020	0 9551	0 0838
RWST	1 073	0 044	0 9574	0 0947
ROL	0 213	0 013	0 9633	> 0 1000
ROW	0 640	0 083	0 9852	> 0 1000
RWI	0 505	0 052	0 9788	> 0 1000
RWN	0 361	0 038	0 9041	< 0 0100
RPXS	0 215	0 032	0 9757	> 0 1000
RLSS	0 151	0 013	0 9628	> 0 1000
RWM	0 599	0 035	0 9925	> 0 1000
RLLMR	------	------	------	------

N 19 (4 15 0)

Appendix B
Correlation matrix (Pearson) of morphometric variables

Correlation matrix (Pearson) of morphometric variables.

I. Body and head size variables of wild animals (N = 29)

	BM	SVL	TTL	BW	DCL	CW	SL	SW	OL	OW	IOW	LCR	WN	PXS	ML	LMS
SVL	0.929															
TTL	0.936	0.985														
BW	0.942	0.910	0.905													
DCL	0.899	0.984	0.960	0.919												
CW	0.921	0.989	0.966	0.925	0.986											
SL	0.850	0.967	0.937	0.879	0.985	0.922										
SW	0.883	0.982	0.955	0.889	0.981	0.998	0.982									
OL	0.792	0.909	0.873	0.825	0.921	0.921	0.916	0.906								
OW	0.765	0.897	0.870	0.836	0.943	0.919	0.944	0.927	0.848							
IOW	0.874	0.937	0.923	0.912	0.928	0.954	0.917	0.945	0.851	0.862						
LCR	0.840	0.940	0.929	0.890	0.957	0.954	0.945	0.939	0.910	0.938	0.937					
WN	0.885	0.945	0.924	0.900	0.940	0.970	0.939	0.954	0.902	0.877	0.932	0.913				
PXS	0.832	0.944	0.913	0.867	0.963	0.958	0.962	0.962	0.885	0.942	0.905	0.921	0.921			
ML	0.890	0.984	0.962	0.909	0.988	0.986	0.977	0.984	0.912	0.927	0.936	0.946	0.948	0.957		
LMS	0.833	0.953	0.937	0.849	0.969	0.959	0.979	0.956	0.884	0.929	0.905	0.945	0.925	0.940	0.961	
WSR	0.811	0.880	0.861	0.804	0.928	0.886	0.856	0.887	0.869	0.914	0.834	0.826	0.940	0.954	0.973	0.929

II. Ratio variables of wild animals (N = 29)

	DCL	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS	RLSS
RCW	0.524									
RLST	0.731	0.422								
RWST	-0.469	0.199	-0.690							
ROL	-0.750	-0.291	-0.514	0.335						
ROW	0.255	-0.079	0.248	-0.239	0.690					
RWI	0.634	0.600	0.462	-0.024	-0.729	0.414				
RWN	0.372	0.707	0.627	-0.192	0.088	-0.091	0.353			
RPXS	0.387	0.401	0.456	-0.168	0.299	0.293	0.354	0.367		
RLSS	0.094	0.204	0.338	-0.474	0.165	0.196	0.035	0.120	0.084	
RWM	-0.131	0.282	-0.195	0.466	0.131	-0.069	0.044	-0.091	0.151	-0.033

III Body and head size variables of captive non hatchlings (N=120)

	BM	SVL	TTL	BW	DCL	CW	SL	SW	OL	OW	IOW	ECR	WN	PXS	ML	LMS	WSR
SVL	0.922																
TTL	0.914	0.995															
BW	0.938	0.985	0.983														
DCL	0.926	0.997	0.994	0.987													
CW	0.949	0.993	0.990	0.989	0.995												
SL	0.933	0.995	0.992	0.989	0.997	0.996											
SW	0.932	0.996	0.993	0.987	0.997	0.997	0.996										
OL	0.893	0.983	0.984	0.965	0.984	0.978	0.978	0.980									
OW	0.895	0.959	0.949	0.959	0.958	0.959	0.959	0.961	0.939								
IOW	0.900	0.977	0.980	0.977	0.977	0.974	0.980	0.978	0.955	0.937							
ECR	0.910	0.990	0.985	0.978	0.992	0.988	0.990	0.991	0.977	0.956	0.970						
WN	0.913	0.987	0.986	0.990	0.988	0.985	0.988	0.987	0.977	0.955	0.980	0.983					
PXS	0.891	0.962	0.954	0.952	0.964	0.960	0.967	0.962	0.938	0.941	0.941	0.962	0.956				
ML	0.921	0.993	0.991	0.984	0.995	0.991	0.994	0.993	0.980	0.958	0.975	0.988	0.989	0.965			
LMS	0.919	0.987	0.980	0.983	0.990	0.986	0.989	0.988	0.971	0.957	0.967	0.982	0.984	0.960	0.986		
WSR	0.949	0.993	0.992	0.988	0.994	0.997	0.993	0.996	0.975	0.958	0.977	0.984	0.983	0.954	0.990	0.984	
LM	0.901	0.967	0.960	0.960	0.965	0.966	0.965	0.966	0.916	0.901	0.906	0.950	0.966	0.953	0.965	0.964	0.971

IV Ratio variables of captive non hatchlings (N=120)

	DCL	RCW	RLST	RWST	ROL	ROW	RW1	RWN	RPXS	RLSS	RWM
RCW	0.907										
RLST	0.915	0.876									
RWST	-0.628	-0.473	-0.775								
ROL	-0.915	-0.810	-0.883	0.640							
ROW	-0.135	-0.144	-0.217	0.152	0.019						
RW1	0.882	0.843	0.897	-0.631	-0.911	-0.102					
RWN	0.827	0.846	0.905	-0.665	-0.786	-0.063	0.855				
RPXS	0.263	0.244	0.334	-0.284	-0.319	0.213	0.293	0.391			
RLSS	0.058	0.020	0.011	-0.043	-0.062	0.194	0.065	0.067	0.131		
RWM	0.458	0.507	0.318	-0.065	0.354	0.004	0.393	0.273	-0.161	0.389	
RLLMR	-0.191	-0.258	-0.245	0.115	0.123	0.416	-0.221	0.085	0.285	0.360	0.141

V. Body and head size variables of captive hatchlings (N=124)

	BM	SVL	TTL	DCL	CW	SL	SW	OL	OW	IOW	ECR	WN	PXS	ML	LMS	WSR
SVL	0.781															
TTL	0.768	0.938														
DCL	0.701	0.798	0.813													
CW	0.732	0.752	0.793	0.798												
SL	0.444	0.575	0.609	0.713	0.655											
SW	0.626	0.625	0.657	0.696	0.717	0.535										
OL	0.528	0.635	0.615	0.666	0.615	0.729	0.517									
OW	0.345	0.460	0.449	0.538	0.492	0.647	0.413	0.762								
IOW	0.218	0.193	0.221	0.097	0.138	0.268	0.134	0.399	0.278							
LCR	0.267	0.434	0.425	0.524	0.445	0.463	0.357	0.522	0.506	0.034						
WN	0.594	0.614	0.628	0.606	0.585	0.396	0.545	0.485	0.339	0.102	0.176					
PXS	0.270	0.248	0.265	0.270	0.390	0.238	0.212	0.076	-0.006	-0.121	0.046	0.172				
ML	0.764	0.858	0.856	0.842	0.832	0.720	0.679	0.710	0.567	0.215	0.442	0.626	0.324			
LMS	0.530	0.451	0.445	0.492	0.361	0.184	0.437	0.173	0.009	0.035	0.099	0.361	0.198	0.418		
WSR	0.348	0.356	0.402	0.428	0.606	0.215	0.535	0.030	-0.042	-0.151	0.145	0.246	0.415	0.400	0.328	
LM	0.361	0.462	0.574	0.518	0.367	0.298	0.361	0.346	0.327	0.160	0.333	0.408	0.067	0.504	0.394	0.165

VI. Ratio variables of captive hatchlings (N=124)

	DCL	RCW	RLST	RWST	ROL	ROW	RWI	RWN	RPXS	RLSS	RWM
RCW	-0.019										
RLST	0.310	0.185									
RWST	0.268	0.055	-0.832								
ROL	0.171	0.175	0.505	-0.395							
ROW	-0.134	-0.011	0.025	-0.025	-0.251						
RWI	-0.276	0.013	-0.001	0.029	0.011	0.015					
RWN	0.228	0.274	0.415	-0.228	0.355	-0.100	0.076				
RPXS	-0.331	0.297	-0.062	0.085	-0.199	-0.024	-0.013	0.046			
RLSS	-0.093	-0.250	-0.307	0.349	-0.379	-0.125	0.063	-0.202	0.024		
RWM	-0.291	0.208	-0.352	0.426	-0.547	0.014	-0.046	0.312	0.295	0.300	
RLLMR	-0.197	-0.309	0.317	0.209	-0.208	0.125	0.131	-0.160	-0.101	0.329	0.1

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality as a dissertation for the degree of Doctor of Philosophy

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